
THE HISTORY OF NEOTROPICAL VEGETATION: NEW DEVELOPMENTS AND STATUS¹

Robyn J. Burnham² and Alan Graham³

ABSTRACT

The isolation of South America from Central America and Africa during the Tertiary Period left a strong imprint on the flora of the Neotropics. South American Eocene through Miocene fossil assemblages, both pollen and macrofossils, document a rich tropical flora on the continental margins, and represent some of the only data on pre-landbridge lowland taxa in South America. Lowland Miocene floras from Amazonia are remarkably similar in their high diversity to Amazonian floras today based on lists of dominant families. Recent geophysical data on the uplift of the northern Andes show a strong correlation between uplift and the development and diversification of montane forests in Colombia and Venezuela. The emergence of a continuous landbridge at 3 Ma between Central and South America is well documented and is demonstrated by the arrival of temperate elements in South American highlands and concurrent appearance of South American taxa in Central America. There is no evidence for displacement of lowland tropical plants in South America by northern immigrants, which appears to stand in contrast to the published record for mammals. The mix of taxa in extant Mexican tropical floras derived from tropical South America, tropical Central America, and from remnants of northern tropical Eocene floras is strong evidence for the impact that the landbridge through the Panamanian isthmus had on the neotropical flora. The early appearance of low-elevation savannas is inferred from an increase in grass pollen in the middle Pliocene of Panama; however, widespread savannas are not indicated by pollen data from the Central American region. Rather, beginning in the latest Miocene Epoch and continuing up to the Quaternary, a mix of tropical rainforest and mixed tropical woodlands is suggested for the lowlands, based on pollen evidence. Accumulating data on temperature changes during the late Tertiary and Quaternary Periods points to low-latitude temperature fluctuations of up to 6°C. Proposals of accompanying widespread rainfall fluctuations are more equivocal. Rainfall probably varied regionally, resulting in a mosaic of habitats controlled by river migration, sea level fluctuations, local dryness, and local uplift. Zones postulated as refugia provide testable hypotheses using neoecological and paleoecological data. The paleoecological data to test these hypotheses are still limited taxonomically and spatially. It is important to stress that the effect of the isolation of South American neotropical floras has not been erased in the 3 million years since their connection with Central America. New data from middle and late Miocene floras in South America will be critical in determining the degree to which the composition of South American floras has been influenced by immigration of plants from the better-known Central American area to the north.

The neotropics extend geographically from the Tropic of Cancer to the Tropic of Capricorn, including environments as diverse as dry desert or humid rainforest. Mean annual temperatures range from over 30°C to as low as 10°C. Elevations from sea level up to well over 6000 m are included. This wide range of climate and topography has a profound effect on the composition and structure of neotropical vegetation. The area also has a distinctive geographic outline. It is roughly hour-glass shaped, with the narrow isthmus of Panama composing the fragile, primarily lowland connection between large northern and southern land masses. In addition, both the northern and southern neotropics lie contiguous to subtropical and temperate areas to the north and south: no barriers to immigration

from these extra-tropical sources are present. There are as many reasons for neotropic patterns of diversity and distribution today as there are different landforms and climatic regimes. If these differences are played out over the course of the late Mesozoic and Cenozoic, when data from fossil deposits can inform us about the sequence of changes that has taken place, the history of neotropical vegetation takes on a dizzying complexity.

We approach this review of the vegetational history of the Neotropics by outlining four important events (Fig. 1). We initially treat the two major land areas separately, because for much of their history they were indeed isolated from one another. Then, we summarize the interactions that postdate the connection and treat selected aspects of the Neo-

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² Museum of Paleontology, University of Michigan, Ann Arbor, Michigan 48109–1079, U.S.A.

³ Department of Biological Sciences, Kent State University, Kent, Ohio 44242, U.S.A.

A PARTIAL TIME SCALE (CRETACEOUS TO PRESENT)

ERA	PERIOD / SUBERA	EPOCH/ STAGE	Million Years Before Present	NEOTROPICAL EVENTS		
CENOZOIC	QUATERNARY	HOLOCENE	0.01	QUATERNARY CLIMATE		
		PLEISTOCENE	1.64			
	TERTIARY	NEOGENE	PLIOCENE	5.2	LANDBRIDGE EXISTS	
			MIOCENE	23.3		
		PALEOGENE	OLIGOCENE	34	ISOLATION	
			EOCENE	56.5		
			PALEOCENE	65		
			MAESTRICHT.	74		
		MESOZOIC	CRETACEOUS	CAMPANIAN	88.5	ISOLATION
				SANTONIAN		
CONIACIAN						
TURONIAN						
CENOMANIAN	97					
ALBIAN	112					
APTIAN						

Figure 1. Time scale for the mid-Cretaceous to Present showing the four events discussed in the text. Note that the events are not temporally distinct from one another.

tropics as a whole up to the present. The unique history of the vegetation of the Neotropics is, in large part, due to the geographic isolation of its southern half during most of the past 90 million years, subsequent uplift of the Andes, and interactions between the northern and southern elements.

We review data on the pollen and macrofossil records from the late Cretaceous Period up to about 5000 years ago, when climates and physiography took on essentially modern aspects. We address the Neotropics as geographically defined: from 23° South to 23° North latitude. At the southern extreme we have included fossil floras from Bolivia, but have excluded floras from Argentina, Paraguay, and southern Brazil. At the northern extreme, we have included fossil floras from Mexico up to 23° North latitude. Our review of the history of the vegetation in this broad geographic area incorporates all the published data known, insofar as it can be integrated into databases on plant macrofossils and microfossils. Figure 2 shows the location of pub-

lished fossil floras from Costa Rica to Bolivia, which are referenced in Appendix 1.

A BRIEF HISTORY OF THE ACCUMULATION OF
MACROFOSSIL AND MICROFOSSIL
DATA IN THE NEOTROPICS

Among the oldest reports of plant fossil assemblages from the Neotropics are the works of T. Wolf, a geologist who mapped areas of southern Ecuador in the late 1800s in company with G. vom Rath (Wolf & vom Rath, 1876). His work on paleontology and geology in southern Ecuador coincided temporally with the explorations on extant plant biology of Richard Spruce in the Amazon and Andes. Wolf's reports of fossils from the inter-Andean basins of southern Ecuador were followed by H. Engelhardt, who published several taxonomic treatments of plant fossils from 1887 through 1895. From about 1915 through 1945, E. W. Berry published extensively on neotropical paleobotany with works on macrofossil floras from Mexico through Patagonia (Berry, 1921a, 1929a, 1945a). Berry

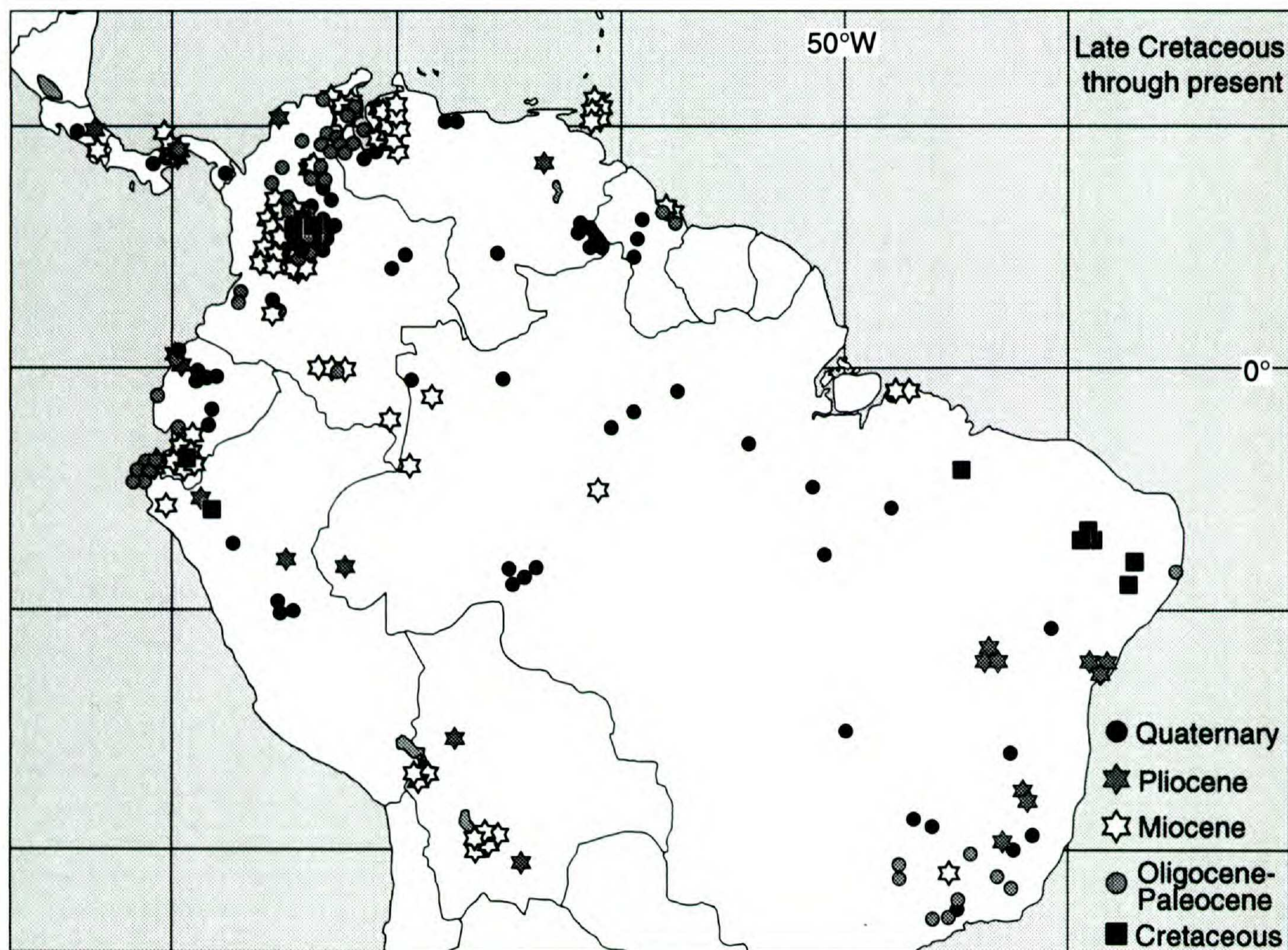


Figure 2. Distribution of published fossil plant localities in northern South America and southern Central America of Late Cretaceous to Quaternary age, referenced in Appendix 1.

published more than 55 papers on South American paleobotany alone, detailing the systematic affinities of the floras and reconstructing vegetation, altitude, and paleoclimate. Although Berry's treatments of the floras were classic for the time, his identifications were based on a comparatively small

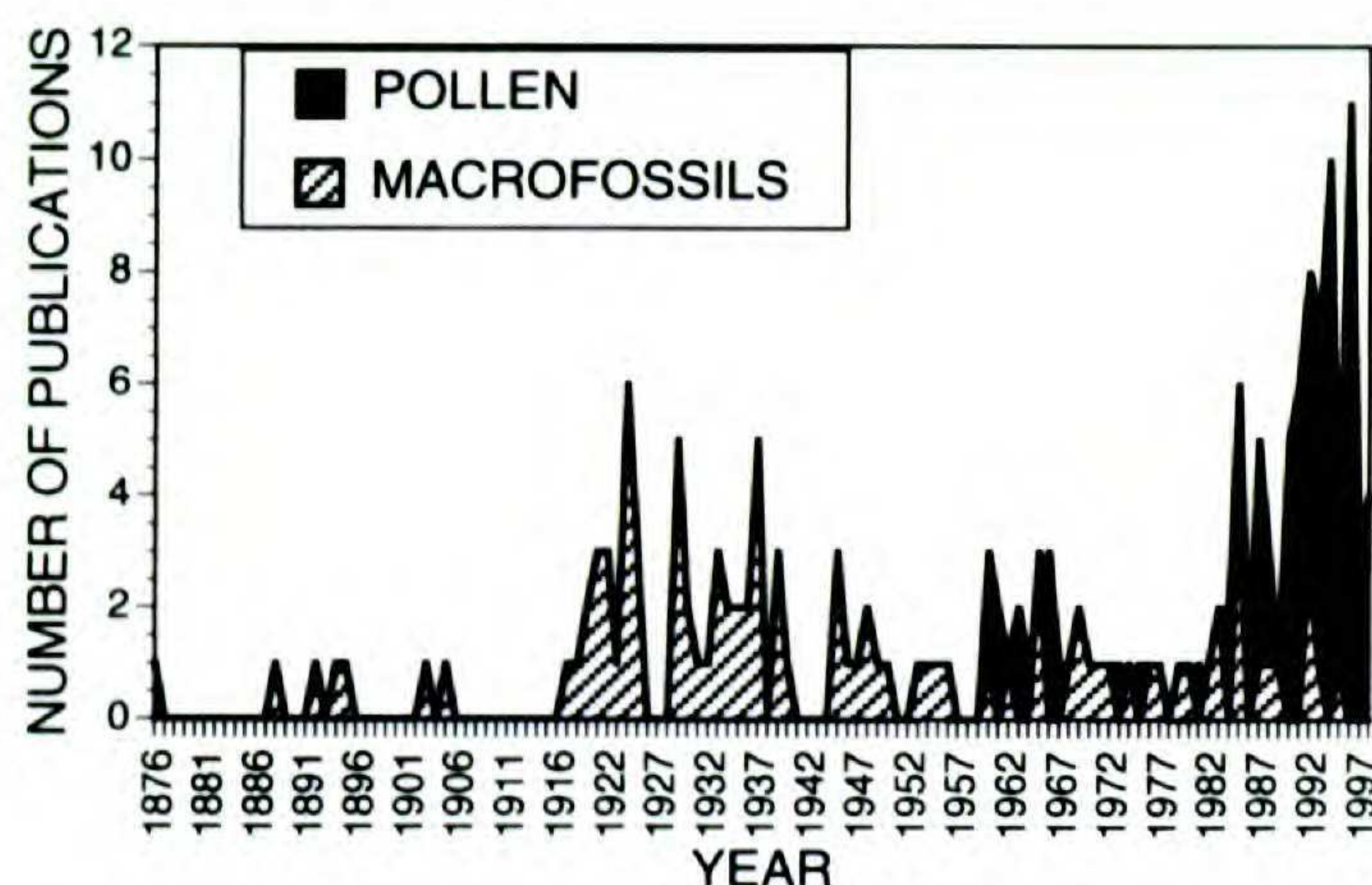


Figure 3. Publication activity in neotropical paleobotany since 1876. Publications are coded with respect to the dominant organ reported: all macrofossils (leaves, fruits, seeds, wood) are grouped. Publications listed are primary reports of localities and fossil plant remains; no summaries or reviews are included.

number of known modern taxa. His firsthand experience in South America appears to have been quite limited. Berry's identifications of Eocene fossil plants from the United States may be at least 60% in error (Dilcher, 1974), and it is also a concern that pollen samples processed from the same Costa Rican localities (Graham, 1987) turned up none of the genera identified by Berry (1921a). Nonetheless, the paleobotanical literature was dominated by Berry's publications on the Neotropics up to the time of his death (Appendix 1).

After Berry there was a relative lull in publication activity (Fig. 3) until palynology became an established research tool in tropical America. In 1954 the first of the monumental works of T. van der Hammen on vegetation reconstruction, using palynology of the Colombian Andes, was published (van der Hammen, 1954). Some of this work used artificial, form-generic taxonomy, making comparisons with macrofossils difficult. However, other research was focused on creating a pollen zonation for the High Plain of Bogotá. From the dominant taxa, reconstructions of vegetation zones were achieved and directly related to the uplift of the northern Andes.

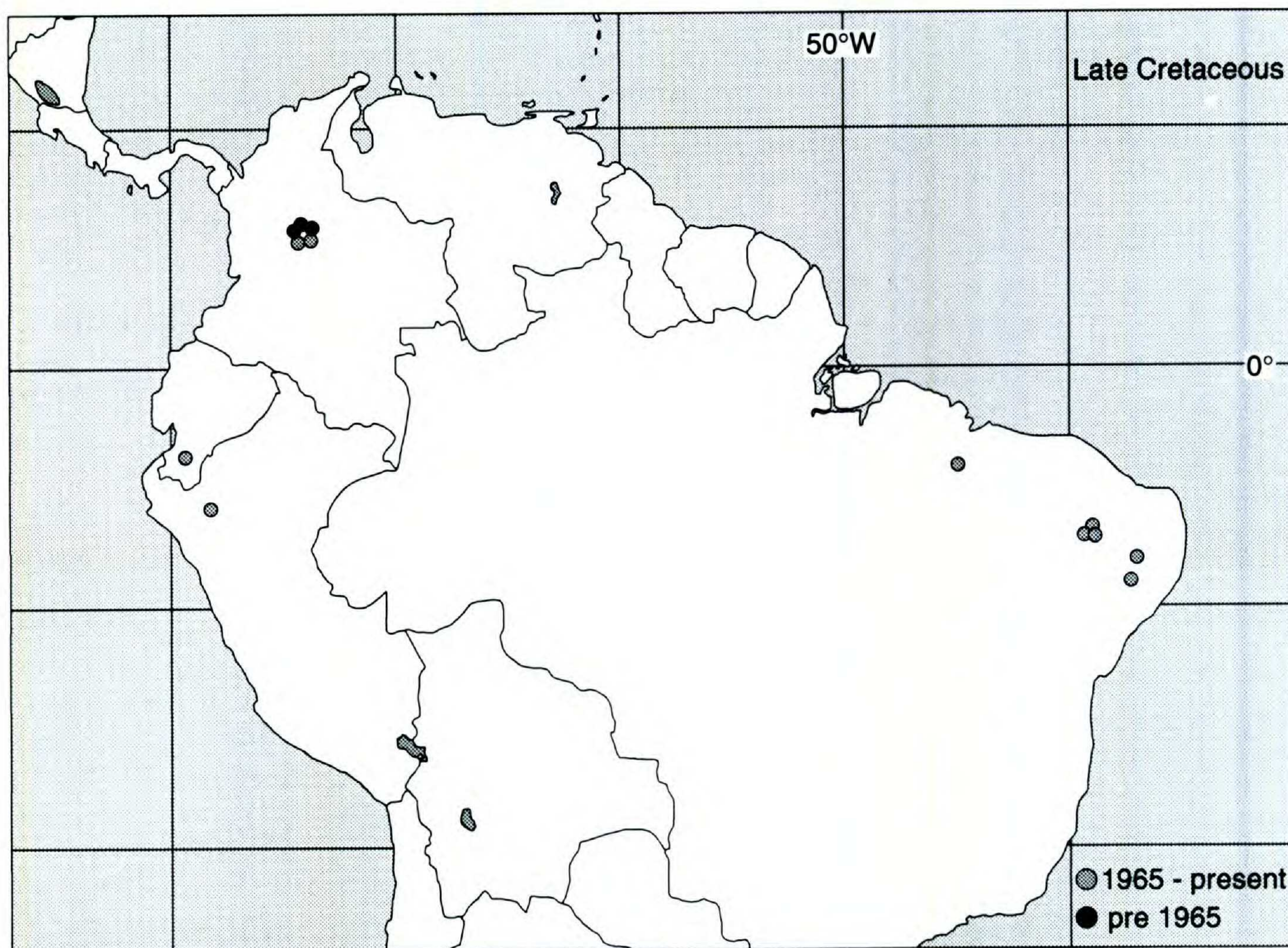


Figure 4. Distribution of published fossil plant localities in northern South America and southern Central America of Late Cretaceous age.

The potential for assessing the nature of past vegetation depends upon the methodologies of macrofossil paleobotany and paleopalynology. Each has its strengths and weaknesses. Pollen provides an inventory of many canopy trees, shrubs, and understory herbaceous plants, identifiable mostly to genus, and is useful for reconstructing larger-scale vegetational patterns (tens of square kilometers of vegetation may contribute to a single sample). Macrofossils provide an inventory mostly of canopy trees and shrubs, identifiable to species, and allow detailed reconstruction of vegetation in the immediate vicinity of the depositional basin; less than a square kilometer of vegetation usually contributes to a single fossil assemblage (Burnham, 1994). Clearly, the integrated use of both methodologies creates the highest resolution picture of vegetation and vegetational change. Although pairing of samples from localities is a logical goal, it is only rarely that such studies have been carried out in paleobotany (Hollick, 1928; Graham & Jarzen, 1969; Leopold & MacGinitie, 1972; Farley & Dilcher, 1986; Farley & Wing, 1989; Taggart & Cross, 1990; Skog & Dilcher, 1994; Willard et al., 1995; Wijninga, 1996a).

DISTRIBUTION OF THE DATA IN TIME AND SPACE

In Figure 2 we show the geographical distribution of data used in this review. Localities from which fossil floras have been described, either with a goal of vegetation reconstruction or floristic census, were plotted and coded for the geological time period represented. Sites shown on these maps are listed by country and stratigraphic position in Appendix 1. The distribution of sites mentioned in the text in Mexico, Central America, and the Antilles are presented in publications by Graham (1988c). In South America there is a clear preponderance of localities on continental margins. Amazonia is particularly poor in pre-Quaternary sites, and it is important to continue exploration for additional palynological or macrofossil assemblages in the rich Cenozoic deposits (Tschopp, 1953; Duarte, 1972, 1983, 1985).

We have also displayed the data for northern South America in two categories: pre-1965 and post-1965 (Figs. 4–8). This distinction is entirely arbitrary, chosen only on the basis of a visible break in publication activity at 1965. In addition, radiometric dating was being widely applied by this

time, and some tropical Cenozoic floras could be dated independently of the estimates based on the fossil assemblages. Thus the two categories also reflect greater possibility for independent age confirmation in the more recently published works.

FOUR MAJOR EVENTS STRUCTURING
NEOTROPICAL VEGETATION

EVENT I: ISOLATION

The physical setting

Geophysical and biological evidence now indicate that rifting between Africa and South America was under way by about 95 mya (Pitman et al., 1993; 106–84 mya, Goldblatt, 1993). By 85 million years ago, it is estimated that a seaway covering as much as 10° longitude (up to 800 km) existed between the two southern continents. Plant communities in South America of this age are too fragmentary to provide much evidence on the degree of isolation of the floras of the two continents. However, from other regions we know that angiosperms were diversified by this time (Muller, 1981, 1984; Wing et al., 1993), and several modern families are recognizable (Wolfe & Upchurch, 1987; Friis & Crepet, 1987). The ecological dominance of angiosperms in most habitats becomes apparent after the Cenomanian (Wing & Tiffney, 1987a, b; Wing et al., 1993).

At the same time that Africa and South America were separated, South America was also isolated from North America by a marine portal through Central America. This condition had existed since the inception of the Tethys seaway (Early Jurassic) and continued until the emergence of the Panamanian Landbridge in the Late Pliocene. Thus, notwithstanding the possibility of small-scale chance dispersal events, South America from about 100 to about 3 million years ago was an island continent (McKenna, 1980; Simpson, 1980; Marshall et al., 1982; Simpson & Neff, 1985; Webb, 1985; Marshall, 1988). The isolation of South America attracted the attention of vertebrate paleontologists because fossil mammals in South America, older than the connection with North America, were easily distinguished from their northern counterparts. Paleobotanists were slower to recognize the discontinuities, perhaps because the extant angiosperm flora of northern South America and Central America was bewilderingly diverse to Northern Hemisphere plant biologists, but also because many plant collections from South America were limited and this provided few opportunities for comparison. In addition, Berry was not an adherent of the theory

of continental drift (Sullivan, 1974; Graham, 1988c), a situation that did not encourage critical comparison of the fossil floras of the two continents. In fact, theories on the origin and development of the biogeographic affinities of the South American flora were derived more through study of the modern flora (Raven & Axelrod, 1974; Gentry, 1982a, b, 1990; Simpson & Neff, 1985) rather than through the efforts of paleobotanists of the time (but see reviews by Taylor, 1991, 1995). Thus, the meager history of comparison of floristic patterns between Central and South America may be due to the high diversity of the floras and an early lack of acceptance of the concepts of continental drift.

Floristic similarity between northern and southern Neotropics

Fossil angiosperm floras in northern South America older than 65 mya are few (Fig. 4). More are available for assessing the degree of isolation from fossil floras of early Tertiary age (Fig. 5). The majority of the reported floras are from Colombia, Venezuela, and Ecuador, with over half published before 1965. To the north, well-preserved early Tertiary pollen floras are reported from Panama (Graham, 1985, 1999a) and Mexico (Martinez-Hernandez et al., 1980). The percent similarity between palynomorphs in Early to Middle Eocene pollen floras from Panama and northern South America was calculated by Graham (1992) and is reported here in Table 1. The low degree of floristic similarity (2.6%) is in accord with the physical reconstructions of the Panamanian landbridge (Coates et al., 1992; Coates & Obando, 1996), as well as with the data on the distinctiveness of mammalian faunas at that time. The taxonomic determinations made on the leaf floras are either limited in number or too unreliable to reconstruct vegetation types in the Paleocene. Recently, however, Eocene mangrove vegetation flanked by inland palm

Table 1. Similarity of palynomorphs between Central and South America from the Early Eocene Epoch through Quaternary Period.

Time period	Similarity of palynomorphs between Central America and South America
Early to Middle Eocene	2.6%
Early Miocene	10.7%
Middle Pliocene	8.9%
—Landbridge established—	
Quaternary	29.7%

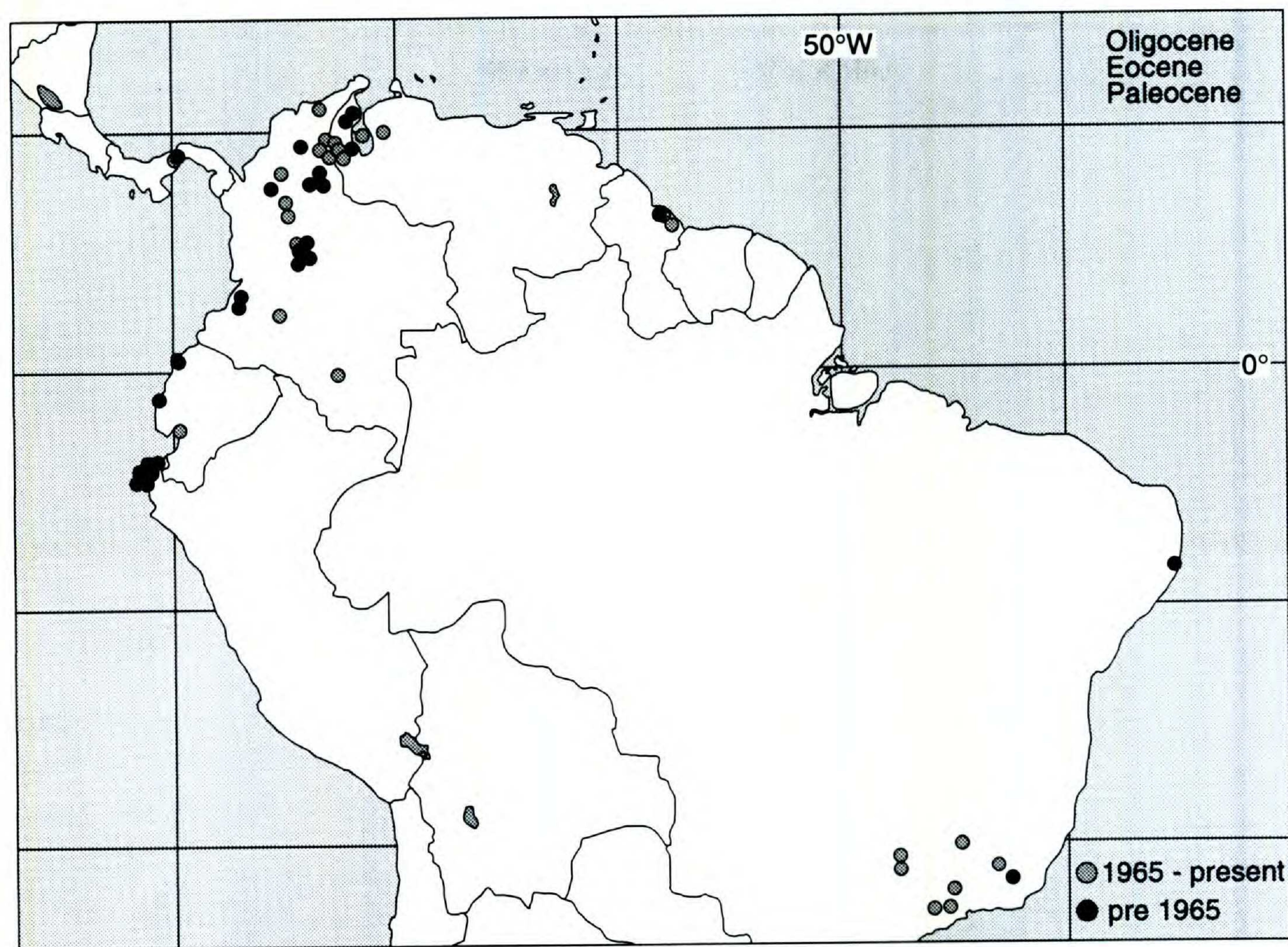


Figure 5. Distribution of published fossil plant localities in northern South America and southern Central America of Paleocene through Oligocene age.

and dicotyledon-dominated forests has been reconstructed by Rull (1998a) from the northern coast of South America.

Disjunctions recognized in modern distributions

The isolation of South America during the Tertiary Period can also be inferred from the distribution of extant taxa as presented by Gentry (1992), Wendt (1993), and Hammel and Zamora (1990, 1993). The predicted diversity for a group of plants isolated in South America until establishment of the landbridge would be a high number of species in South America, with only a few, perhaps widespread, taxa extending into Central America. This pattern was documented for many genera by Gentry (1982b) and more recently for *Serjania* sect. *Platycoccus* by Acevedo-Rodriguez (1993). Such a pattern, however, might also derive from narrow ecological amplitudes in the restricted taxa and wider ecological amplitudes in the geographically wide-ranging taxa. Nonetheless, in many of the cases cited by Gentry (1982a), the ranges of South American taxa extend north into Colombia, but not across the Isthmus of Panama. This suggests that a recent

geographic barrier is responsible for many of the observed patterns.

Fossil and modern family diversity

During the period of isolation, northern South America harbored a rich assemblage of angiosperm families. The high diversity of Amazonian forests today is due in part to recent speciation and immigration of taxa from Central America starting 3 million years ago, but the high diversity within prominent neotropical families most likely is due to the long evolutionary history of many taxonomic groups in South America. Although Tertiary fossil floras from Amazonia are few, none of them completely documented, and most from moderate paleoaltitudes (probably close to 1000 m), fossil assemblages of Miocene deposits from southern Ecuador (Berry, 1929a, 1945a) do reveal family-level diversity. Fossil taxa were assessed only at the family level because the identifications by Berry have been repeatedly questioned over the past 40 years. Floras from these basins are currently under study by one of us (RJB), and our research on Berry's family-level taxonomic determinations shows

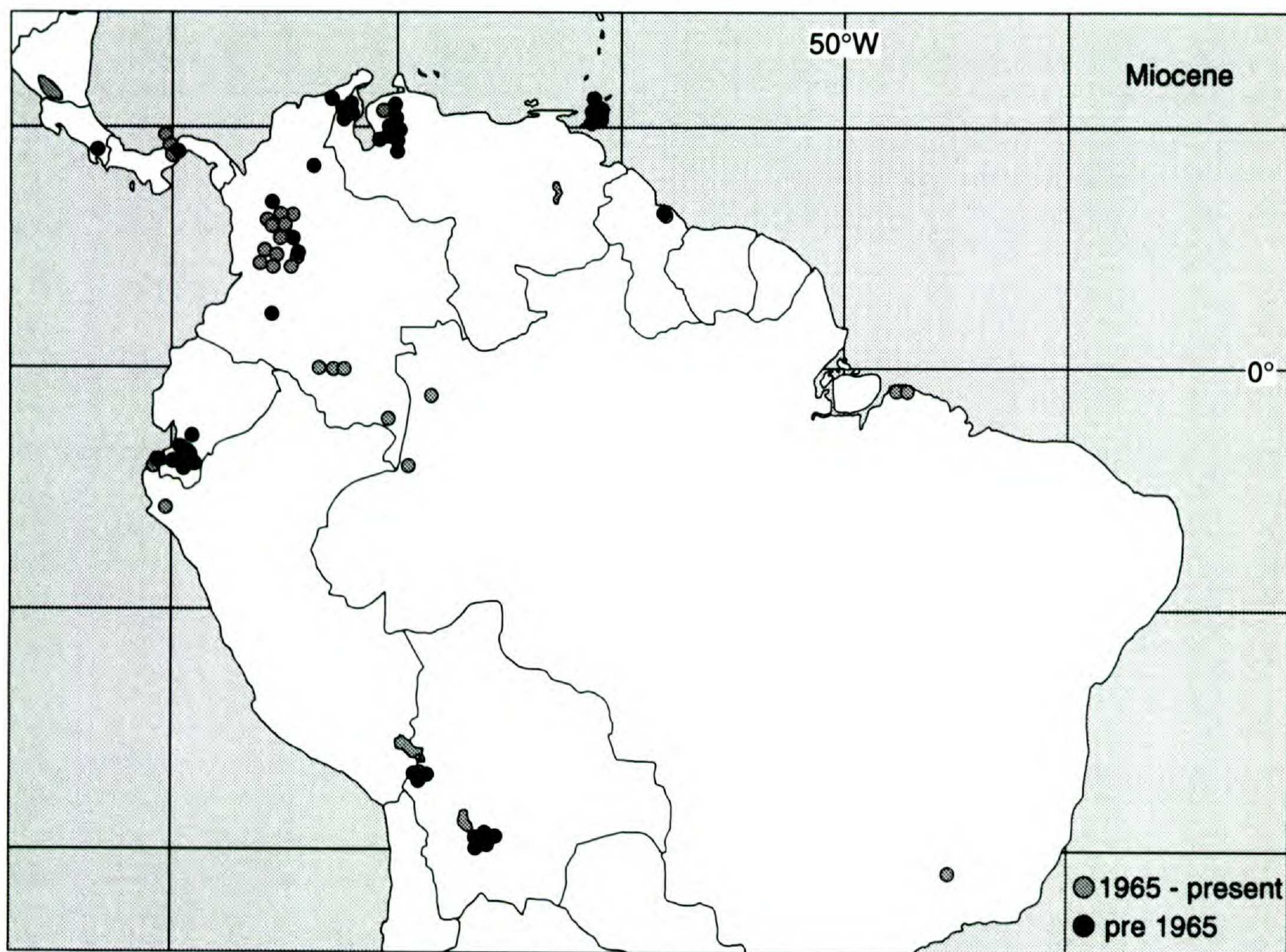


Figure 6. Distribution of published fossil plant localities in northern South America and southern Central America of Miocene age.

that they are reasonable in about 70% of the cases. Four modern lowland tropical floras were reported (Gentry, 1990) in which the percentage of species in 20 angiosperm families are listed, and these can be compared to the proportion of species in the same families of fossil plants from Ecuador (Fig. 9). At this crude level of comparison, the most common angiosperm families in the four modern Amazonian forests are also represented in the fossil assemblage. Similarly, Rull (1998a) indicated that the Eocene mangrove communities of northern Venezuela were similar in diversity and composition to other equivalent-age mangrove floras worldwide. Hoorn (1994a) reported Miocene palynological diversity in Amazonian Colombia that is at least as high, if not higher, than modern diversity in the area today (see also discussion by Hooghiemstra & van der Hammen, 1998). Lundberg and Chernoff (1992) and Lundberg (1997) reported that freshwater fish diversity in Middle Miocene deposits of Colombia was probably as rich as in the fish faunas from Amazonian basins today. Mammalian diversity was also high before the interchange (Marshall, 1985; Marshall & Cifelli, 1990).

Endemism as an effect of isolation

A pattern expected from the isolation of a land-mass for a considerable amount of time is a high level of endemism. This is well documented on islands. For example, the island continent of Madagascar includes close to 10,000 endemic plant species due in part to its isolation from Africa since the mid-Cretaceous (Takhtajan, 1986). The 3 million years of contact between Central America and northern South America has certainly decreased the extent of endemism in both areas, but high endemism in some groups still can be documented. Table 2 lists genera with at least three species that probably evolved in South America and are endemic there today. Genera known from the Tertiary fossil record in South America are indicated. Likewise, Wendt (1993) listed genera that may have diversified in Central America or Mexico and are endemic there today.

EVENT II: UPLIFT AND PHYSIOGRAPHIC CHANGE

The second important time in northern South America is the period from about 15 million years

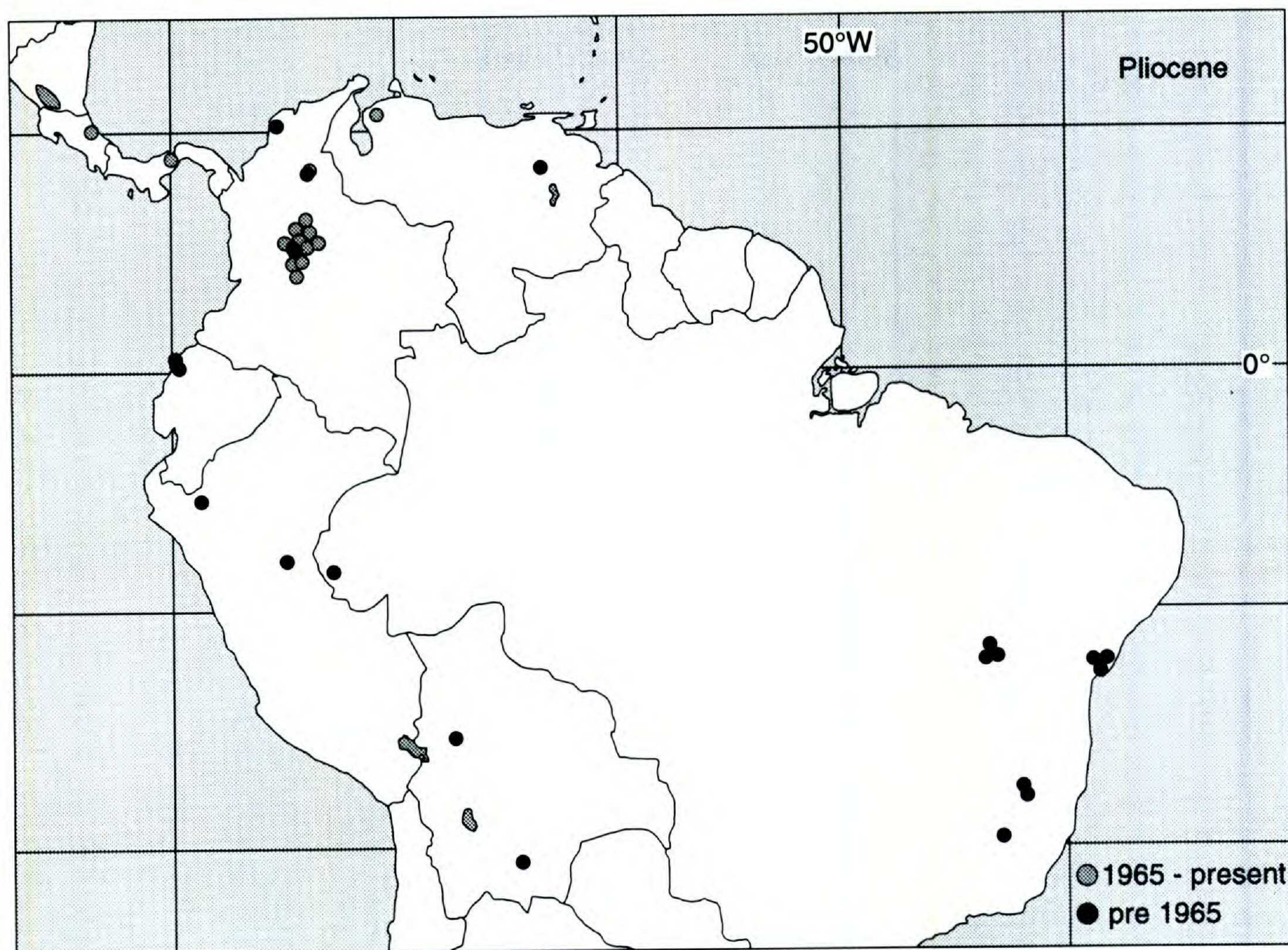


Figure 7. Distribution of published fossil plant localities in northern South America and southern Central America of Pliocene age.

ago to the present. Note that this phase, including uplift of the Andes and changing drainage patterns, overlaps with the younger period of landbridge connection and also with the older period of isolation. Part of the difficulty in interpreting the present vegetation in South America derives from events that overlap. This underscores the care that must be taken in attributing patterns noted in modern distribution to recent fluctuations in climate.

Altitudinal changes

The major period of uplift in northern South America occurred in the Miocene Epoch, although there is strong evidence for uplift in the central and southern part of South America earlier than the Miocene Epoch (Jordan & Alonso, 1987; Sempere et al., 1990). Exact altitudes are difficult to determine because this requires latitudinally paired lowland and upland equivalent-age floras that can provide lapse rates or enthalpy estimates (and thus altitudes: Wolfe, 1992; Forest et al., 1995; Gregory-Wodzicki, 1997; Gregory & McIntosh, 1996). Despite the large number of floras studied by Berry,

few are tied to radiometric dates, and many appear to be from areas of moderate paleoelevation. Lowland coastal or lowland Amazonian floras exist in Colombia, Ecuador, Peru, and Brazil, but these have not been studied or are not tied to well-established biostratigraphic sections.

The paleophysiography in western Colombia has been reconstructed as an elongated peninsula with a mountainous backbone. Elevations during the middle Miocene Epoch in the northern Andes have been estimated by palynological records from the High Plain of Bogotá as being less than 700 m, while by the late Miocene Epoch the area is estimated to have been close to 1000 m (Wijninga, 1996b). Middle Miocene sediments in central Colombia preserve the exquisite La Venta mammal fauna, interpreted to indicate lowland tropical conditions (Kay & Madden, 1997) probably below 500 m. Situated on the eastern cordillera of the Colombian Andes, the mammal fossils and their sedimentary environments indicate that uplift began as early as 12.9 mya (Guerrero, 1997). The La Venta sites would be ideal for calibrating up-

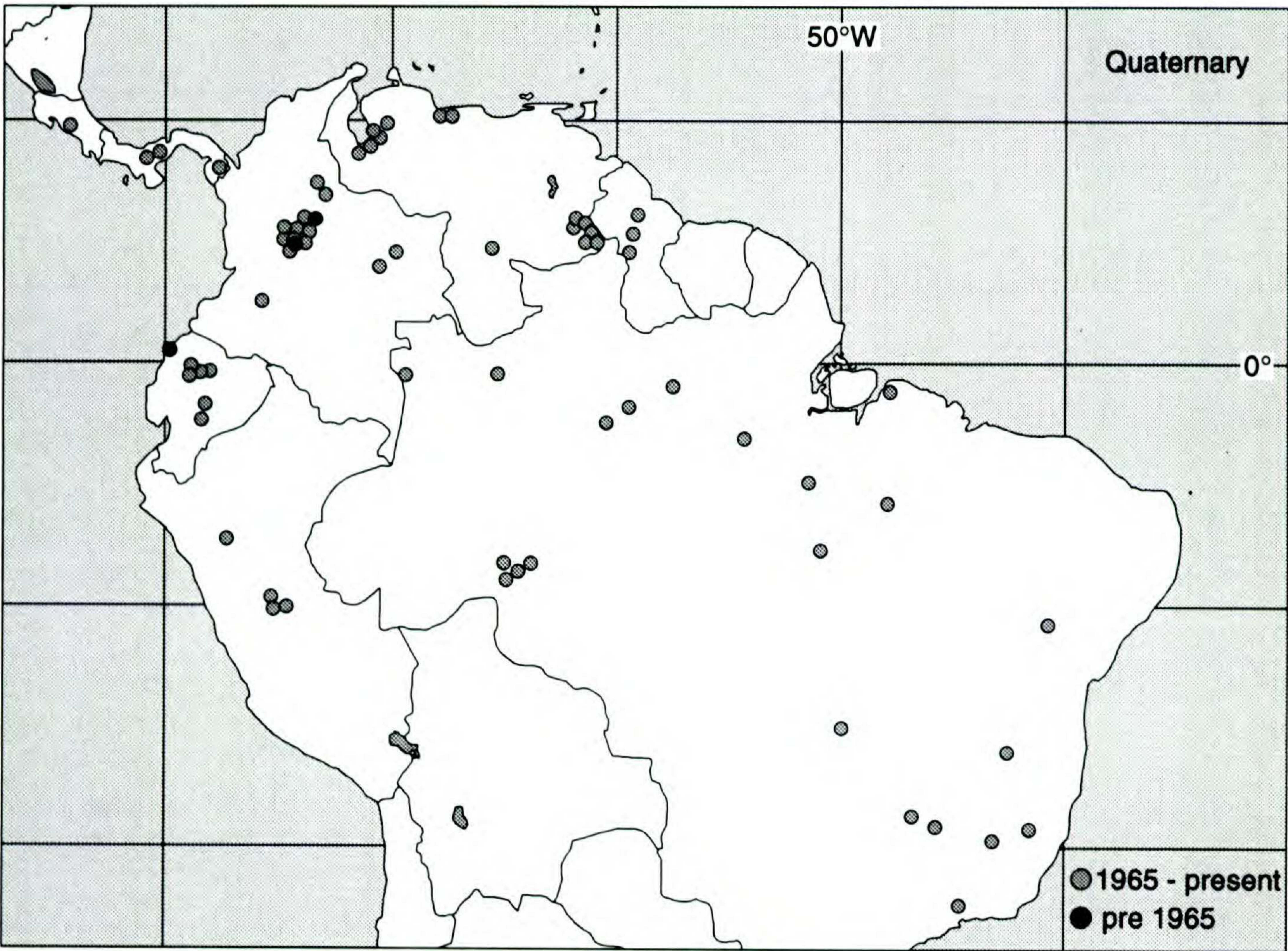


Figure 8. Distribution of published fossil plant localities in northern South America and southern Central America of Quaternary age.

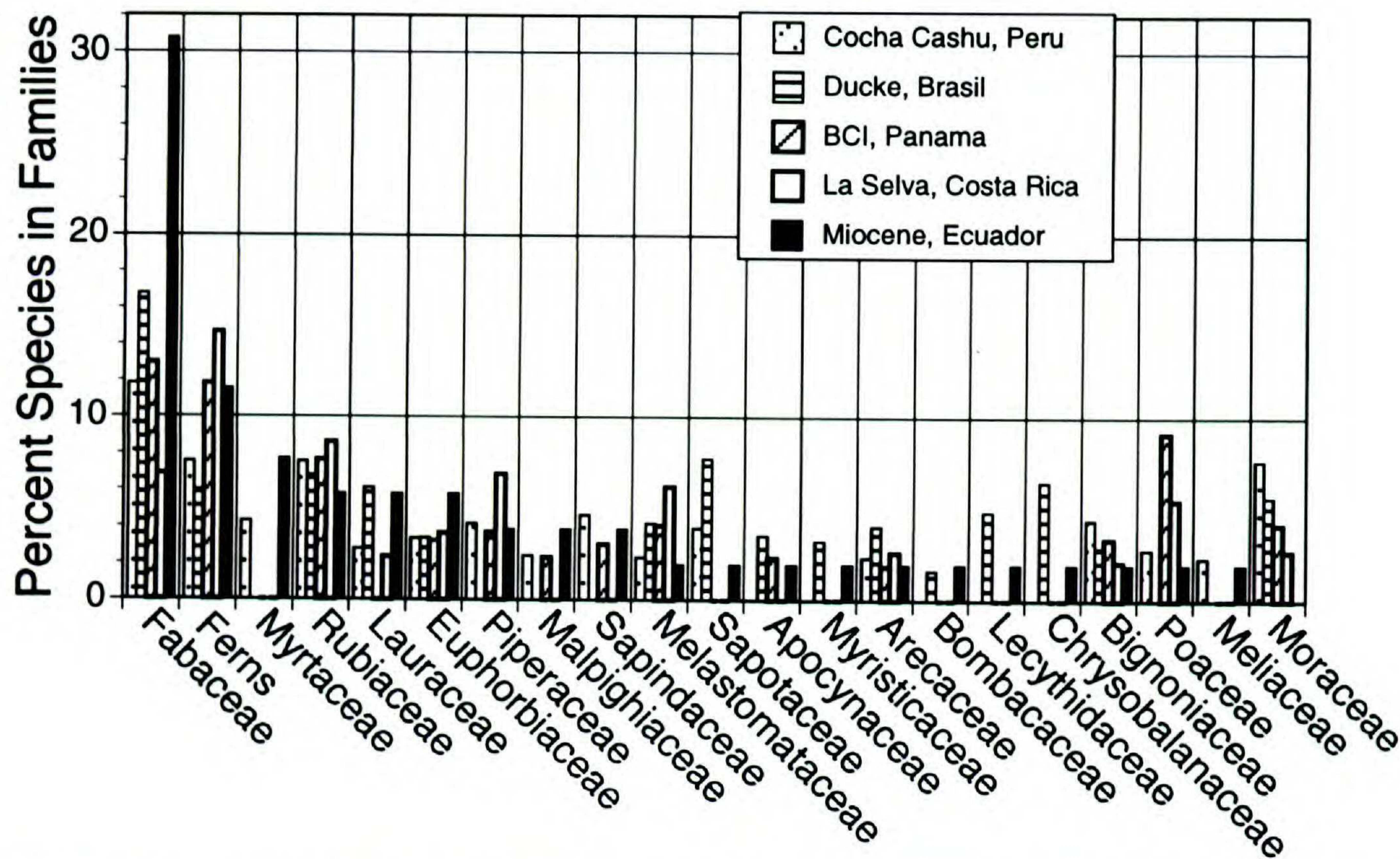


Figure 9. Comparison of modern and Miocene neotropical floras using proportional species diversity within families at all sites. Modern floral data from Gentry (1990).

land floras if fossil leaf floras could be recovered from this volcanically influenced terrane. Fossil wood from the area was reported by Schönfeld (1947). Fish faunas dating from the middle Miocene Epoch and preserved in the present Magdalena Valley of Colombia document a strong affinity to current Amazonian freshwater fish faunas. This indicates that the Eastern Cordillera of Colombia had not created sufficient barriers to migration of fish until at least 11 mya (Lundberg & Chernoff, 1992).

Drainage and physiographic change

Reconstructions of the physiography of northern South America presented by Hoorn (1994a, b, 1995) and by Vonnhof et al. (1998) and synthesized by Kay and Madden (1997) show that in the early Miocene Epoch, the Western Cordillera of Colombia was high enough to deflect sediment in an eastward direction and potentially isolate the current Choco region. The major sediment source to the Amazon Basin was from the moderately uplifted Guyana Shield (Fig. 10). A controversial portal (Marañon Portal) in the area of Guayaquil has been proposed (Nuttall, 1990; Hoorn, 1994a), but by the middle Miocene Epoch, the Andes in southern Ecuador probably no longer allowed westward transport of sediments from the Amazon Basin to the Guayaquil area (Vonnhof et al., 1998). Instead, primary sediment flux was northeastward, with sediments directed toward the major depositional basin off the coast of present eastern Venezuela. Currently, the Andes provide the bulk of sediments to the Amazon and Orinoco systems, with the largest sediment flux now directed east to the Amazon mouth, rather than north toward the Orinoco.

The simplified physiography presented here suggests that the middle Miocene is the time during which the distinctive nature of the flora in the Choco region began its development. Habitat diversity in the Choco region was probably higher in the mid-Miocene than suggested by Gentry (1982a), which would give a much greater age to the endemism documented there today. The Choco, including coastal Ecuador, was isolated from the Amazon by the rising Andes and from Panama by the deep trench off the northwestern coast of Colombia.

Evidence from palynology

Certainly the most useful paleobotanical research in northern South America in the past 50 years is that of T. van der Hammen, H. Hooghiemstra, and their associates at the University of Amsterdam (summarized in Hooghiemstra & van der

Hammen, 1998). The palynological work of Hoorn (1994a, b) and Wijninga (1996a, b) addressed the eastern and central regions of Colombia, respectively. Hoorn documented a variety of habitats including palm swamps, riparian vegetation, and diverse tropical forests in eastern Colombia. Flooding was common, and the majority of sediment came from the east. She also presented strong evidence for vegetation change due to uplift in the Andes during the middle to late Miocene (Hoorn, 1994b). Wijninga, whose work involved sediments of middle Miocene through late Pliocene age, indicated that in the present High Plain of Bogotá lowland conditions existed through the end of the Miocene Epoch. Lowland forests developed on well-drained floodplains. Higher elevations supported only lower montane forests. By the early Pliocene sub-Andean taxa appeared on the present High Plain of Bogotá, along with the pollen of a few high-Andean taxa, which were interpreted as coming from nearby highlands. Wijninga (1996a) documented the progressive uplift of the Andes through the Pliocene using a combined pollen and macrofossil approach. Analysis of the upper stratigraphic sequence was presented by Hooghiemstra (1994), who documented the arrival of northern temperate taxa (see below).

The effects of the changing drainage patterns in northern South America are also preserved in strata at the mouths of the major rivers. One such study (Diaz de Gamero, 1995) indicated that in the early through middle Miocene the proto-Orinoco River built a delta in northern Venezuela, east of the Maracaibo Basin. Through uplift of the Eastern Cordillera of Colombia, the river was deflected progressively eastward during the late middle and late Miocene. This uplift to the west of the depositional center isolated the floras of western Colombia, as well as fragmented and diversified habitats that previously existed as contiguous tropical lowland swamps.

Evidence from plant macrofossils

The record of Miocene plant macrofossils in northern South America is seemingly rich, with 50 published reports. However, much of this work was completed prior to 1960, and lacks a modern systematic and plate tectonic perspective. One of us (RJB) has recently initiated macrofossil plant studies in Ecuador and Bolivia (Burnham, 1995a, b). Three Miocene basins in southern Ecuador and two in Bolivia are under investigation. The three Ecuadorian basins each include 55–75 species of fossil plants, of which most are dicotyledonous angio-

Table 2. Selected Gondwanan-derived genera, still primarily endemic to South America today. Estimated number of species per genus is indicated in parentheses. Only genera with at least three species are listed. * indicates Tertiary fossil record in South America.

Trees	Lianas and vines
<i>Amaioua</i> (25)	<i>Clytostoma</i> (9)
* <i>Apeiba</i> (10)	<i>Mansoa</i> (15)
<i>Campomanesia</i> (80)	<i>Maripa</i> (19)
<i>Catoblastus</i> (17)	<i>Selysia</i> (3)
* <i>Coussapoa</i> (30)	<i>Siolmatra</i> (3)
<i>Crematosperma</i> (17)	<i>Apondandra</i> (4)
<i>Cyclolobium</i> (5)	<i>Dicella</i> (6)
<i>Ecclinusa</i> (21)	* <i>Trigonia</i> (24)
<i>Geoffroea</i> (3)	
<i>Herrania</i> (20)	
<i>Hexachlamys</i> (3)	
* <i>Humiria</i> (4)	
<i>Jessenia</i> (6)	
<i>Leonia</i> (6)	
* <i>Loxopterygium</i> (5)	
<i>Parapiptadenia</i> (3)	
<i>Peritassa</i> (14)	
<i>Ptilochaeta</i> (5)	
<i>Seguieria</i> (6)	
<i>Schinopsis</i> (7)	
<i>Siparuna</i> (150)	
<i>Socratea</i> (5)	
* <i>Thinouia</i> (12)	
* <i>Ticorea</i> (3)	

sperms. Species richness is high in some localities (up to 33 species). Over 80% of the species in each basin bear entire-margined leaves, and the leaf size is about 35% notophyll, 40% microphyll, and the remainder evenly divided between very small and very large leaves. Provisionally identified angiosperms from the Cuenca Basin are: *Loxopterygium* (Anacardiaceae), *Tipuana* (Fabaceae: Burnham, 1995a), *Coussapoa* (Cecropiaceae), Lauraceae, Malpighiaceae, and Arecaceae, while the Nabon Basin includes *Tipuana* (Fabaceae), *Roupala* (Proteaceae), Sapindaceae, Clusiaceae, and Melastomataceae. The Loja Basin was studied by Berry (1929a, 1945a); taxa from that basin verified by recent work include *Coussapoa* (Cecropiaceae), *Trema* (Sterculiaceae), *Tipuana* (Fabaceae), *Ruprechtia* (Polygonaceae), Meliaceae, Lauraceae, and Malpighiaceae.

The Miocene basins of southern Ecuador are well suited to provide information on the rate of uplift and degree of influence of a rain shadow in the northern Andes during the middle Miocene. All three floras have been tied to radiometric dates ranging from 13 to 10 mya (R. H. Madden, unpublished data). Mean annual paleotemperature indi-

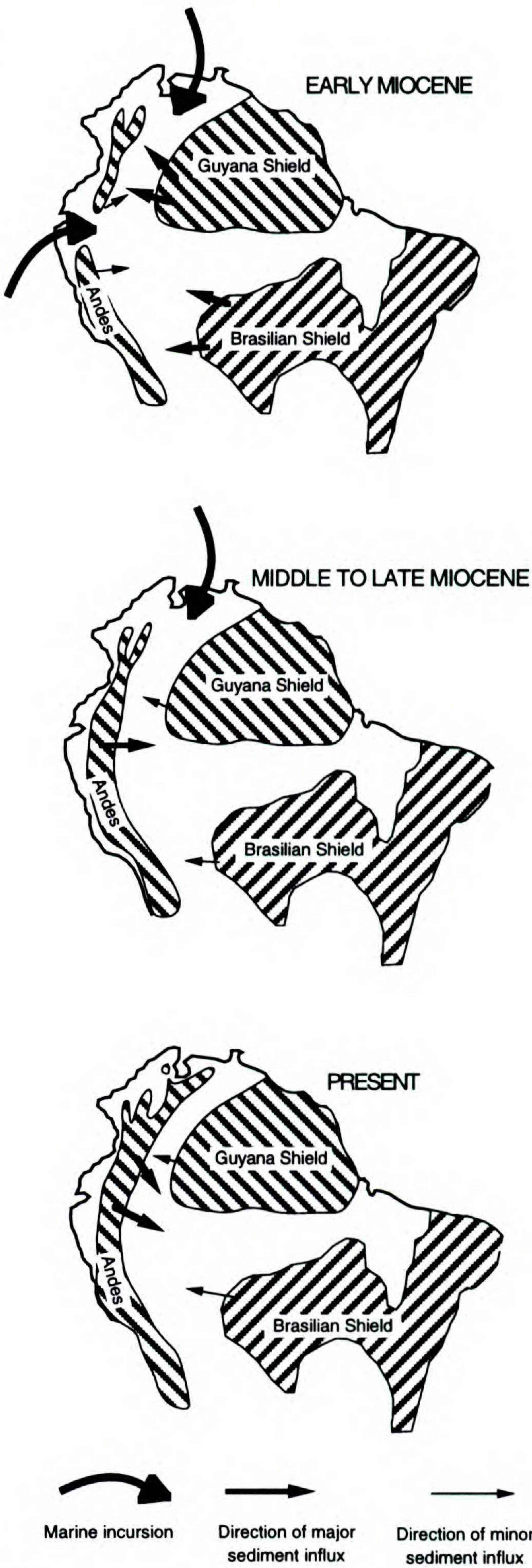


Figure 10. Major sedimentary sources, highland areas, and seaways in Early Miocene, Middle to Late Miocene, and Present South America. From Hoorn (1994b).

cated by leaf margin analysis varies among the basins from 22 to 28°C. All plant-bearing deposits include a large proportion of small leaflets of Fabaceae (up to 30% of the species), which may indicate a seasonally dry climate. Of the three sites, Loja has the largest-leaved species indicating relatively wetter conditions based on correlations of leaf size and precipitation in modern floras (Wilf et al., 1998). Like today, Loja may have been to the east of the Andes, whereas the other two basins may have been between rising parallel chains of the Andes. This eastern position would have diminished the effect of a rain shadow on the flora of the Loja basin.

Changes in physiography and its effect on vegetation are well documented in sections from Colombia, but new evidence from the Pebas formation in eastern Peru (Räsänen et al., 1987, 1995) indicates that changes dating to the middle Miocene are present throughout northern South America. Indeed, as noted by Guerrero (1997), the time of uplift of the Eastern Cordillera of Colombia was a period of global importance, which included the closure of the east end of the Mediterranean seaway; the collision of the Australian plate with Indonesia, thus closing the faunal gap recognized as Wallace's line; the deep sea sedimentation hiatus at 12.0–11.8 Ma reported by Keller and Barron (1987); and a major cooling event that expanded the Antarctic Ice Cap (Woodruff et al., 1981). Increases in the seasonality of precipitation have been cited from many areas, which would have substantially increased habitat diversity at this time.

EVENT III: CLOSURE OF THE ISTHMUS OF PANAMA

Physical changes

The formation of land connections between North and South America had profound climatic (Burton et al., 1997) and biogeographic consequences for the flora and fauna of both continents. Prior to the middle Miocene at ~15 Ma tropical marine waters interchanged between the Atlantic and Pacific Oceans, and there was only weak marine-water transport northward via the Gulf Stream. At ~15 Ma a sill began forming in the Isthmian region that intensified flow of the Gulf Stream. This provided warm water to the North Atlantic region that together with Milankovitch orbital cycles, and decreasing atmospheric CO₂ concentration from waning plate tectonic activity, eventually produced conditions favorable to the development of glacial climates.

Interchange of flora and fauna

Of particular biogeographic importance for the floral and faunal interchange is the timing of the formation of the Panama landbridge. This has been estimated recently from three independent sources: provincialization of eastern Pacific/Caribbean marine biotas (Coates & Obando, 1996; Coates et al., 1992; Jackson et al., 1996), interchange of terrestrial mammals between North and South America (Stehli & Webb, 1985; Webb & Rancy, 1996), and the similarity between palynomorphs on either side of the Isthmus at different times during the Cenozoic (Graham, 1992).

Through the middle Miocene (16–15 Ma) there were marine passages across present-day Central America, and deep-water sediments and biotas are especially evident between the southern (eastern) terminus of proto-Central America and the cordillera of northwestern South America (Fig. 11). By the late Miocene (7–6 Ma) marine portals were more restricted (Fig. 12), and by the late Pliocene (~3 Ma) they existed only across the eastern and western extremes of the Isthmus (Fig. 13). Sedimentological and marine invertebrate provincialism date the establishment of an essentially complete structural connection between North and South America at between 3.5 and 3.1 Ma (Coates et al., 1992; Coates & Obando, 1996). Sometime after 3.5–3.1 Ma the interchange of terrestrial organisms lacking means for long-distance dispersal was facilitated by the development of land corridors that were elevated above the low-lying coasts and marshlands. Although waif dispersal events prior to 3.5 mya have been noted (Reig, 1980; Gingerich, 1985; Gentry, 1992; Marshall & Sempere, 1993; Webb & Rancy, 1996), there is no conclusive evidence that a continuous terrestrial corridor existed between Central America to South America prior to the late Pliocene, about 3 to 3.5 mya.

Recent summaries of the mammalian fossil record provide important information on the climates, kinds of habitats, and the time of appearance and expansion of the terrestrial corridors. First, the affinities of the Early and Middle Tertiary faunas of Central America are almost exclusively with North America, while the relationship of the modern fauna is with South America. This was recognized early on by Wallace (1876): "The portion of North America that lies within the tropics (Mexican Subregion) closely resembles the [Brazilian Subregion] in general zoological features," and he noted "unmistakable evidence of an extensive immigration from South into North America, not long before the Glacial epoch" (quoted from Webb & Rancy, 1996:

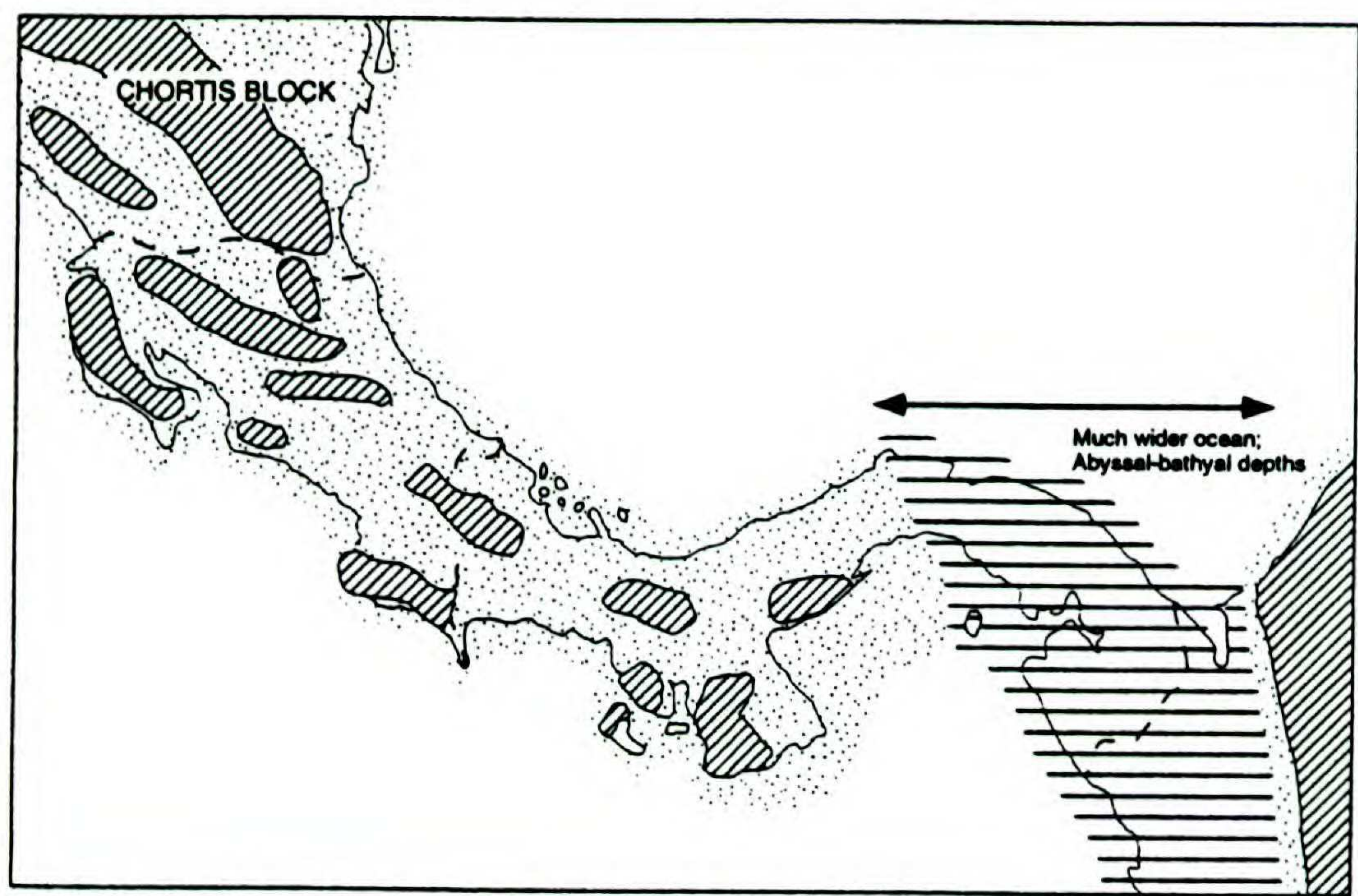


Figure 11. Central American Isthmus during the middle Miocene (16–15 Ma). Oblique parallel lines = emergent land; dots = shelf sediments; parallel lines = abyssal oceanic sediments. From Coates and Obando (1996). Used with permission of the University of Chicago Press.

335–336). Second, large numbers of immigrants from North and Central America are first found in South America after the establishment of the land-bridge. Relatively fewer, but still a large number, of South American mammal genera are first noted in North and Central America after the landbridge was completed. These Pliocene migrants were mostly characteristic of temperate climates and savanna habitats. Evidence from fossil mammalian faunas is further interpreted to suggest that by the middle Pleistocene the savanna corridor was giving way to tropical rainforest, especially during interglacial times (Webb & Rancy, 1996: 348).

The flow of mammalian immigrants from north to south appears to have been larger than from south to north (Marshall et al., 1982; Webb, 1985). In addition, there appears to have been a higher speciation rate among taxa that moved to the south, compared to the northward-moving immigrants (Fig. 14). Thus, in addition to different numbers of species successfully migrating in each direction, there were also different rates of subsequent diversification among mammalian taxa involved in the interchange. This resulted in the asymmetrical pattern of distribution among extant North and South American mammals. According to Webb (1991),

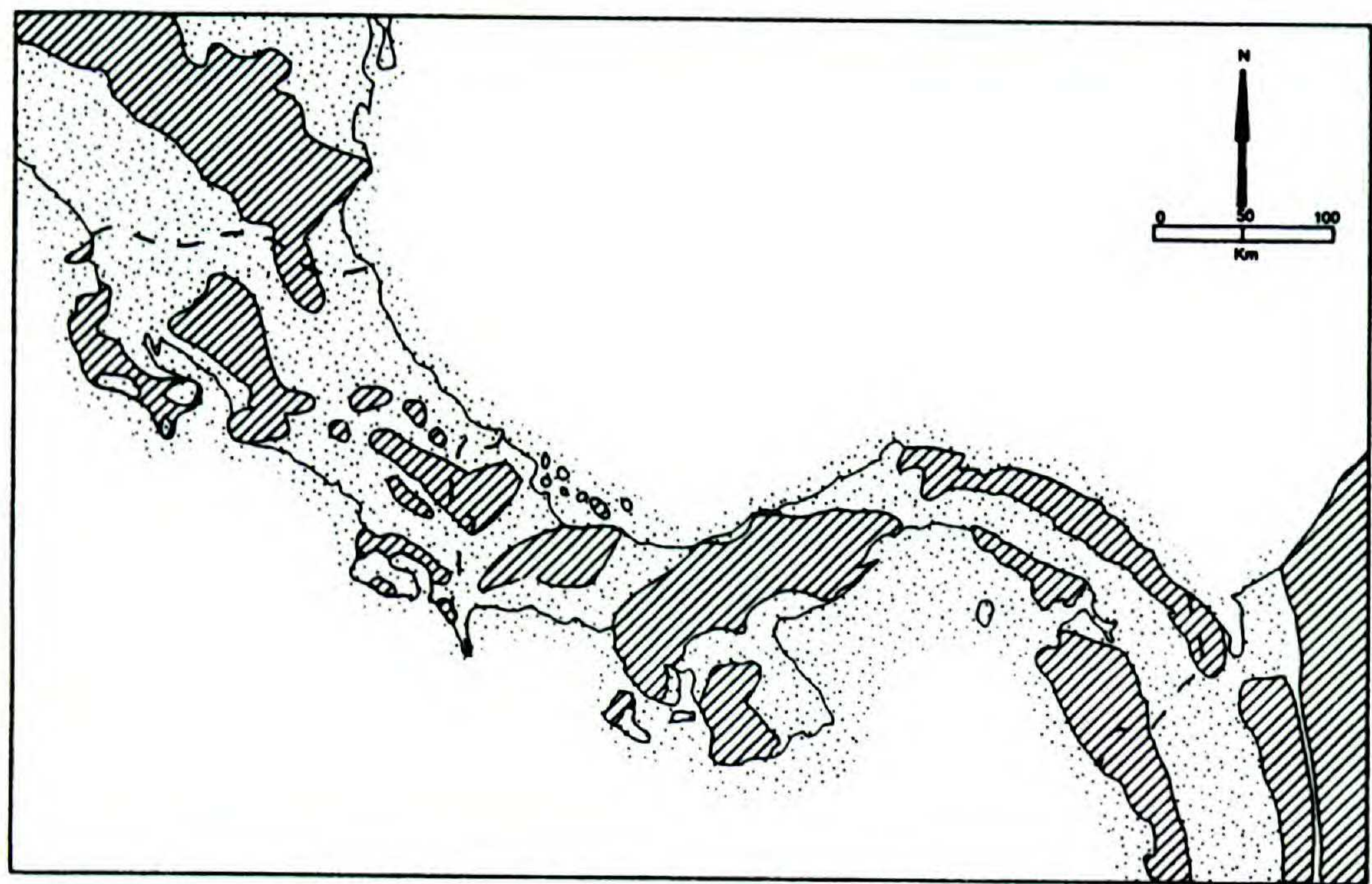


Figure 12. Central American Isthmus during the late Miocene (7–6 Ma). Symbols and source as in Figure 11.

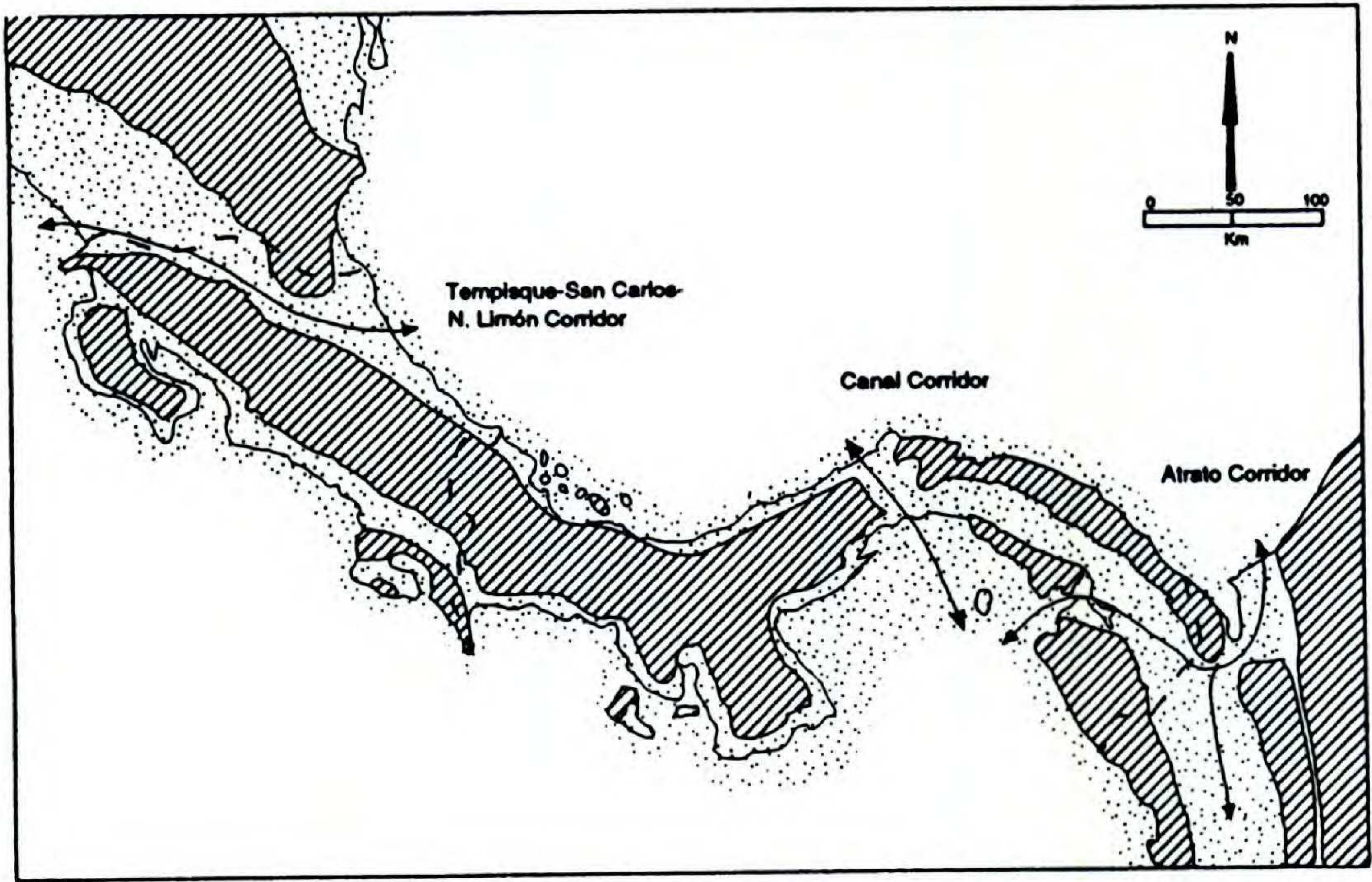


Figure 13. Central American Isthmus during the late Pliocene (~3 Ma). Symbols and source as in Figure 11.

roughly 53% of the extant South American mammal fauna is derived from descendants of immigrants from North America, while only 10% of the extant mammalian fauna of North America is ascribed to descendants of the interchange.

An early introduction from the north into South

America, near the end of the Miocene Epoch, was a raccoon known from the late Miocene of Argentina (Webb, 1985), while two genera of South American ground sloths appear in the late Miocene of North America. By the late Pliocene and Pleistocene, the number of land mammals of northern or-

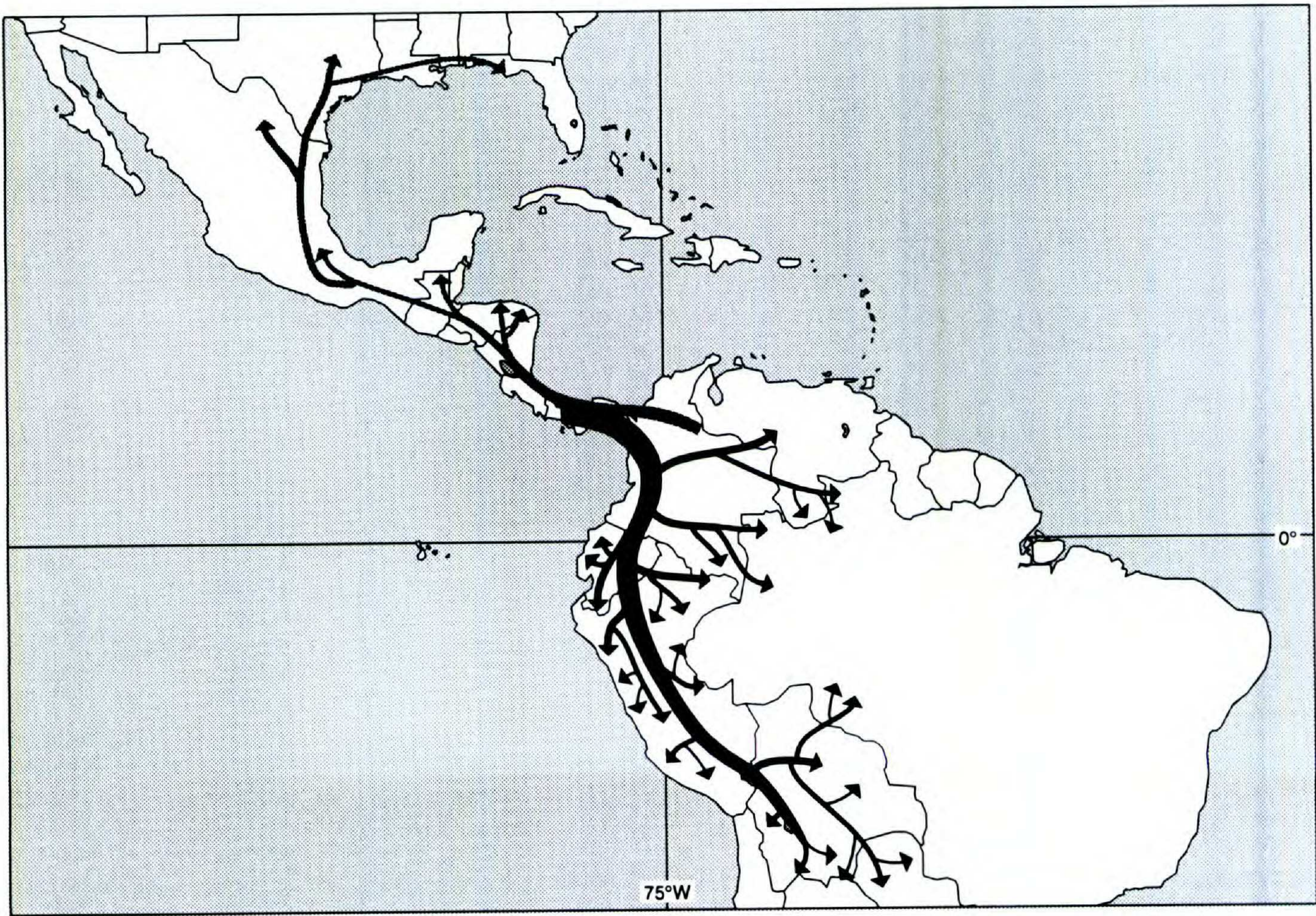


Figure 14. Mammalian migration and diversification following establishment of the Central American landbridge.

igin in South America increases to 15 families and 29 genera (Webb, 1985: table I). These include modern, extinct, or ancestral genera of the Chiroptera (bats), Soricidae (shrews), Leporidae (hares), Heteromyidae (pocket mice), Geomyidae (pocket gophers), Sciuridae (squirrels), Sigmodontine rodents (field mice), the first introduction of Carnivora–Felidae [cats; *Smilodon* (New World Pleistocene saber-toothed tiger), *Puma*, *Panthera*, *Felis*], Mustelidae (weasels, skunks, otters), Canidae (fox and wolf), Procyonidae (raccoons), Ursidae (bears), Gomphotheriidae (elephantids), Tapiridae (tapirs), Equidae (horses), Tayassuidae (peccaries, pig-like forms), early Camelidae (camel line), and Cervidae (deer).

Groups moving from South America into Central and North America include the Dasypodidae (armadillos), Mylodontidae (sloths), Glyptodontidae (an extinct group related to the armadillos), Erethizontidae (porcupines), Hydrochoeridae (capybara), Trichechidae (manatees), Phorusrhachidae (large predaceous ground birds), Megatheriidae (giant ground sloths), Megalonychidae (large extinct edentate mammals), Camelidae (represented by llama-like camelids), Didelphidae (opossums), and Toxodontidae (rhino-like ungulates).

The mammalian record indicates that connections suitable for the migration of dry-land species across the Isthmus were essentially complete by ~2.5 Ma. According to Webb and Rancy (1996), savanna habitats were at least locally available at that time. The origin of the modern tropical mammalian fauna of Central America is placed at approximately the middle Pleistocene or ~780 ka.

The Cenozoic fossil plant record also reflects distinct South American and Central American vegetation through the early and middle Tertiary. As noted previously here (Table 1), in the early to middle Eocene only ~2.6% of palynomorphs are common to assemblages on both sides of the Isthmus. In the early Miocene the figure is 10.7% and decreases to 8.9% in the middle Pliocene. The decrease correlates with rising sea levels during a middle Pliocene interval of increasing warmth (Cronin & Dowsett, 1991). The various factors that affect the calculations are discussed by Graham (1992), and it is especially important to note that they represent similarities in palynomorphs and not in vegetation directly. In the original tabulations, the percent similarity for the late Quaternary (15.7%) was especially approximate because most of the few studies available from Central America were from the lowlands (e.g., Bartlett & Barghoorn, 1973, Panama; Bush & Colinvaux, 1990, Panama; Horn, 1985, off-shore Costa Rica; see also Phillips

et al., 1997), while many of those from northern South America are from the highlands of Colombia (Hooghiemstra, 1984; Hooghiemstra & van der Hammen, 1993; van der Hammen & Hooghiemstra, 1995; 2000–4000 m). However, studies from upland deposits in Central America (Hooghiemstra et al., 1992, Iselbe et al., 1996, Costa Rica, 2310 m; Martin, 1961, Costa Rica, 2400 m) and from the lowlands of Amazonia (Colinvaux et al., 1996a, b; Liu & Colinvaux, 1988; van der Hammen & Absy, 1994) allow new calculations from comparable localities. Appendix 2 lists 235 palynomorphs reported from Quaternary deposits on both sides of the Isthmus of Panama. Seventy of the palynomorphs occur both in southern Central America and in northern South America for a similarity value of 29.7%. Thus, the paleobotanical trend is consistent with that of the marine invertebrate record, tectonics, and mammalian fossil faunas. The floras are distinct until late in the Tertiary (through about the Mio-Pliocene interval) with greater similarities developing in the Plio-Pleistocene and especially in the Pleistocene.

Habitats of the interchange

The fossil plant data are also generally consistent with estimates of habitats (savannas) and climate (temperate) based on mammalian fossil faunas, but with some differences. The paleobotanical evidence indicates predominantly tropical forest throughout the Cenozoic, with restricted grassy savannas developing in about the late Miocene. The early Miocene microfossil floras from Panama (Culebra, Cucaracha, La Boca; ~9°N latitude; Fig. 15) and Costa Rica (Uscari; ~10°N latitude) contain virtually no pollen of the Gramineae, while in the Mio-Pliocene Gatun flora of Panama, grass pollen reaches a maximum of 7.5%. This marks the beginning of at least local savannas that presumably continued to develop through the Pliocene, and expanded during glacial intervals, as reflected by the increase in grazing and browsing members of mammalian faunas. However, in the Cenozoic pollen floras from southern Central America, the dominant components of the paleovegetation are tropical forest elements. This apparent inconsistency between mammalian faunas indicating open savanna vegetation, and paleobotanical evidence for mostly closed tropical forest, is paralleled in the Tertiary record of northwestern North America. There the explanation appears to be frequent disturbance of the vegetation by ash falls associated with extensive volcanism (Cross & Taggart, 1982; Taggart & Cross, 1990; Taggart et al., 1982). This was interpreted as a



Figure 15. General location of fossil palynofloras mentioned in the text.

shifting mosaic of open, short-lived habitats sufficient to support mobile herds of browsing and grazing ungulates within a mostly temperate forested vegetation. The frequent ash layers in the Cucaracha Formation of Panama suggests a similar mechanism (Graham, 1988b). Evidence of extensive savanna development is only present in Quaternary floras, but is never abundant in Central America. Comparable data have not yet been presented in South America. Savanna, as recognized today in Central America, may be a Pleistocene development augmented by recent anthropogenic factors.

There is also evidence to suggest that drier habitats supporting more open vegetation began developing locally in the late Miocene and early Pliocene. The early Tertiary floras from southern Central America contain a few elements of dry habitats. By the Mio-Pliocene these elements increase and include 11 taxa that collectively suggest an early form of tropical dry forest—*Poaceae*, *Acacia*, *Allophylus*, *Busera*, *Cedrela*, *Ceiba*, *Combretum*, cf. *Jatropha*, *Posoqueria*, *Pseudobombax*, and *Serjania* (Graham, 1991).

It is likely that these local drier conditions resulted, at least in part, from a developing rain shadow due to increasing elevations during the Tertiary

Period. Through the early Miocene all elements in the fossil floras from southern Central America can be accommodated at elevations between sea level and ~1400 m. By the Mio-Pliocene (Gatun flora) paleoelevations, based on modern analog distributions, had increased to ~1700 m (lower montane moist forest, lower montane wet forest, premontane dry forest, montane moist forest, montane wet forest). Present maximum elevations are 3820 m (Cerro Chirripó) and 3432 m (Volcán Irazú) in Costa Rica, and 3475 m (Volcán Barú) in Panama. The appearance of these highlands in the Mio-Pliocene began to deflect moisture-laden winds from the north and initiated the differentiation between a wetter Atlantic and drier Pacific side, as at present.

The development of temperate habitats in proto-Central America during the Middle and Late Cenozoic is complex. The initial appearance of northern temperate elements is in the Mio-Pliocene Gatun flora of Panama, where a few pollen grains of *Quercus* are first recovered. This corresponds in time to the appearance of the paleoelevations that began differentiating the region into wetter and drier sides. By the late Quaternary pollen of *Alnus*, *Juglans*, *Liquidambar*, *Myrica*, *Quercus*, *Salix*, and *Ulmus* is present in terrestrial Central American

sediments, although *Juglans* and *Liquidambar* in off-shore deposits from Costa Rica (Horn, 1985) may have been transported from farther north. Localized temperate habitats first appear in the Mio-Pliocene and it is likely they resulted, at least in part, from increasing elevations rather than exclusively from marked changes in climate. We assume that the low-lying, peninsular area in question received ameliorating sea breezes and precipitation that may have dampened the global signal of changes caused by trends in CO₂ concentration and solar fluctuations.

Another factor influencing climates, especially along coastal areas, is upwelling. As the Panama landbridge became established, the flow of the Gulf Stream intensified and brought cold bottom water to the surface in some regions. This is a likely explanation for the cooler climates indicated by the middle Pliocene Paraje Solo flora of southeastern Veracruz, Mexico (17°N), during an interval of overall warming (Graham, 1976, 1998b). Ocean circulation, orogeny, lower CO₂ concentrations (van der Berg et al., 1993; Kürschner et al., 1996), concentrations from globally waning post-Mesozoic plate tectonic activity, and solar-induced fluctuations in climate via Milankovitch mechanisms all influenced the Cenozoic history of environments. In proto-Central America a combination of factors periodically produced local conditions suitable for the interchange of temperate biotas of open habitats in the late Tertiary Period. These conditions prevailed especially in the highlands and became more prevalent toward the end of the Tertiary Period.

Comparison of the mammalian and angiosperm records

Comparison of the pattern of migration and speciation between plant and animal groups involved in the exchange across the Panamanian landbridge has received surprisingly little attention. Simpson and Neff (1985) noted the lack of similarity between plant and mammal records but did not expand on the specific patterns in each lineage. The plant data required for such a comparison is based on two sources of information. First, direct fossil evidence from comparison of taxonomic lists of fossil pollen in Colombia and the Guianas with fossil pollen in Panama and Costa Rica (Graham, 1992) as well as comparison of sites of first fossil occurrences of taxa believed to have been involved in the interchange (Taylor, 1988), and second, evidence from modern distributions of plant taxa (Gentry, 1982a, 1992; Hammel & Zamora, 1990, 1993; Wendt, 1993). Raven and Axelrod (1974) and

Table 3. Laurasian genera now in tropical South America. South American species numbers are approximated from guides and floras (e.g., Gentry, 1993; Brako & Zarucchi, 1993; Killeen et al., 1993).

Trees	Shrubs and herbs
<i>Alnus</i> (1)	<i>Ambrosia</i> (?)
<i>Boehmeria</i> (8)	<i>Berberis</i> (32)
<i>Cornus</i> (1)	<i>Erigeron</i> (?)
<i>Morus</i> (2)	<i>Lupinus</i> (171)
<i>Myrica</i> (3)	<i>Ribes</i> (16)
<i>Prunus</i> (19)	<i>Rubus</i> (18)
<i>Quercus</i> (1)	<i>Salvia</i> (76)
<i>Rhamnus</i> (2)	<i>Satureja</i> (26)
<i>Salix</i> (2–3)	<i>Scutellaria</i> (15)
<i>Sambucus</i> (1)	<i>Valeriana</i> (100)
	<i>Vaccinium</i> (9)
	<i>Viburnum</i> (12)

Simpson (1975) documented taxa that, based on extant distribution, must have been immigrants to South America from the north. The list is short, and few genera show radiation following their arrival in South America. Woody plant taxa that are well known for their appearance in South America following establishment of the landbridge include *Alnus*, *Myrica*, *Quercus*, *Cornus*, and *Salix* (Table 3). These genera include only one or a few species in South America (Brako & Zarucchi, 1993), although they can be ecologically important in many Andean areas. Pollen records cannot be used to resolve the issue of speciation in these cases because the pollen cannot be recognized to species. A more evolutionarily successful group of shrubs and herbs includes *Berberis*, *Lupinus*, *Rubus*, *Scutellaria*, and *Viburnum* (Table 3). The South American species of these genera very likely came into existence after their immigrant ancestors reached South America, similar to the radiation proposed within mammalian genera. However, the timing of the immigrant arrival, relative to the establishment of the landbridge, is difficult to establish without direct information from the fossil record. Their arrival could predate the landbridge, and in this case examination of dispersal mechanisms might prove useful. These plant taxa are absent or are recovered rarely from the palynological record, most likely because they are insect-pollinated. The arrival of the successful sigmodontine rodents was proposed to have predated the landbridge (Hershkovitz, 1966; Reig, 1980, 1986; Marshall & Sempere, 1993), but a consensus has not been reached on this point among vertebrate paleontologists (Patterson & Pascual, 1972; Flynn et al., 1985; Marshall & Sempere, 1993). The fact that South American sigmodontines

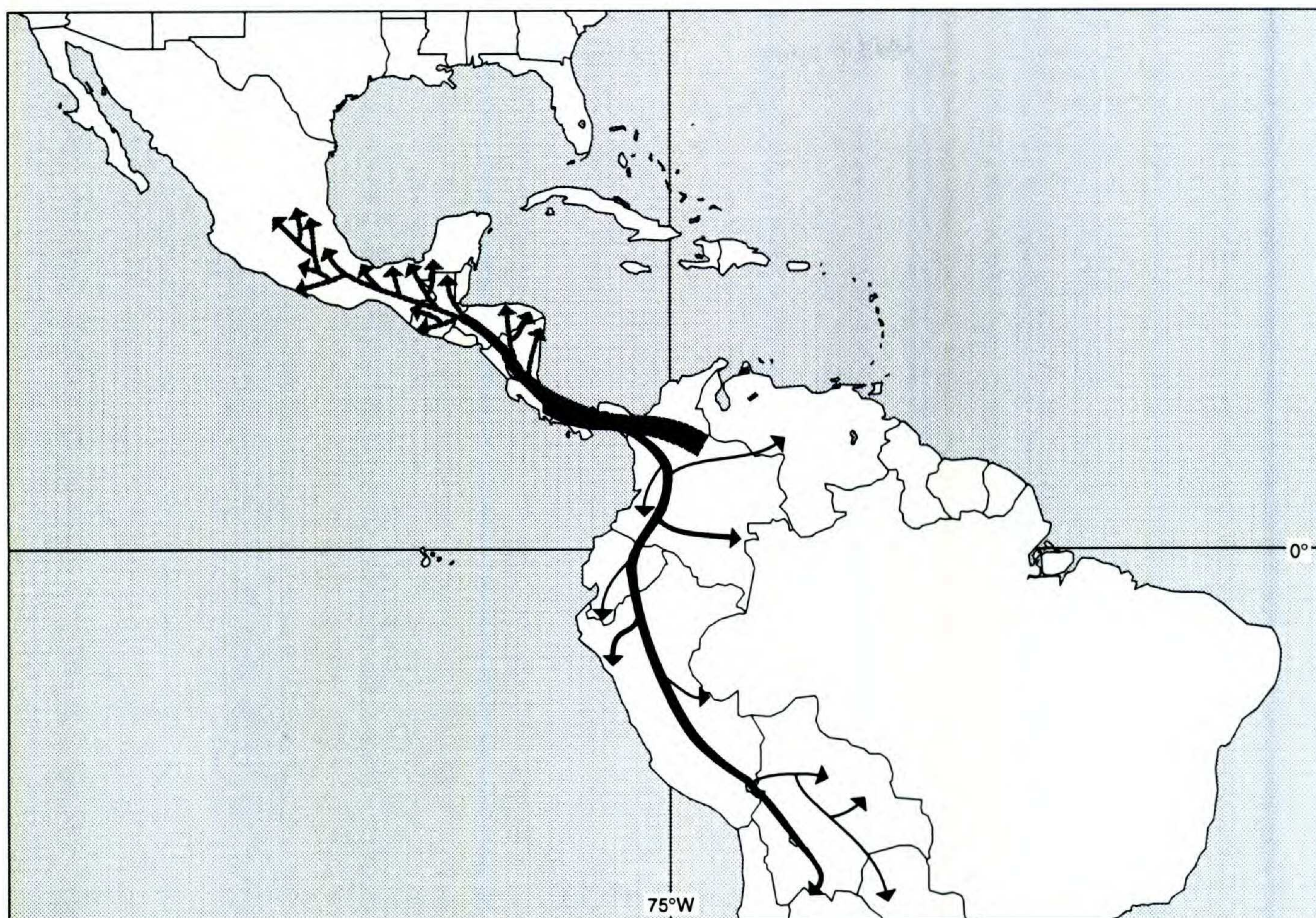


Figure 16. Woody plant migration and diversification following establishment of the Central American landbridge.

appear to be more primitive than North American forms, at least in penile morphology and in host-parasite relationships, casts doubts on their arrival in South America via the landbridge (Jacobs & Lindsay, 1984; B. D. Patterson, pers. comm. 1998). The plant immigration pattern viewed from South America is that establishment of the landbridge resulted in significant changes in the composition of South American upland forests. However, the number of species, and certainly the number of genera descended from northern immigrants, is low. The landbridge appears to have been far less significant for speciation in lowland angiosperms in South America than it was for mammals. To our knowledge, there are no estimates of the number of species in the South American flora that were derived from northern immigrants, but we would place it at about 10%.

From a northern perspective, Wendt (1993) documented taxa based on modern distributions that had most likely immigrated from South America and speciated in Mexico and Central America. These were not compared to the mammalian patterns. Radiations into central Mexico and the Antilles have been suggested by specialists on *Bignoniaceae*, *Malpighiaceae*, and *Sapindaceae* (Gentry, 1992; Acevedo-Rodríguez, 1993, 1996; W.

R. Anderson, pers. comm. 1997). These include radiations into the moist forests of Mexico (Wendt, 1993), but appear to be more typical of the dry tropical forests of Central America, which were widespread until recent deforestation (Janzen, 1988).

In summary, the plant and animal migration and radiation patterns are interestingly different (Figs. 14 and 16). Mammalian radiations in South America are noted in many different groups of larger mammals (deer, canids, camelids, tapirs), but are particularly important among the sigmodontine rodents. These rodents are abundant in many habitats throughout South America, and are perhaps most species-rich in uplands and open habitats (Hershkovitz, 1972). However, when their current distribution is mapped on their phylogenetic diversification it appears that lowland sigmodontines gave rise to highland sigmodontines, rather than being derived from them (Patterson, in press). This contrasts with the situation in plants where uplands do correspond to the site of ecological dominance of the immigrant angiosperms from North America, but in the case of immigrant woody plants, ecological dominance is not accompanied by evolutionary diversification. Once arriving in Central and North America, southern mammals were relatively unsuc-

cessful in an evolutionary sense, where only one or a few species of each group (sloths, capybara, agoutis, and opossums) are found (Emmons, 1990). Conversely, while some northward-moving plants extend just into the wet forests of Panama or southern Costa Rica, the more successful plant groups that extend farther north show strong diversification into the drier, seasonal habitats of Central America. The pollen records that are rapidly accumulating, together with refinements of species lists from both sides of the landbridge, should make it possible to establish the ecological conditions under which taxa migrated. With this added ecological perspective it may be easier to postulate reasons for a particular migration event and the environments in which speciation may have occurred.

Origin of the northern temperate element in neotropical vegetation

Two scenarios have been proposed for the origin of north-temperate plants in Mexico, Central America, and northern South America. One is that many of these elements were part of an ancient widespread vegetation existing in northern Latin America since the Paleogene (Axelrod, 1975). The other is that many migrated southward with cooling climates, the appearance of upland habitats, and the establishment of land connections through the Isthmian region (Graham, 1973). There is also the possibility of random and occasional introductions throughout the Cenozoic by long-distance transport. Three tests are available for assessing the likelihood of each model. First, if there was a general progressive introduction from the north into Mexico, Central America, and northern South America, the oldest temperate plant fossils should be in the north with the younger ones toward the south. Second, the introductions into northern South America should coincide generally with closure of the Isthmus; that is, they should mostly appear in South America after about the Mio-Pliocene. Third, the introductions into northern Latin America should correspond with some global climatic event that favored the southward migration of north-temperate organisms.

In the southeastern United States, pollen similar to *Alnus*, *Betula*, and *Carya* is present in deposits of Paleocene age (Frederiksen, 1991). In the Eocene (Claibornian) there are added *Pinus*, *Castanea*, *Celtis*, *Fagus*, *Quercus*, *Nyssa*, *Juglans*, *Ostrya-Carpinus*, *Platanus*, *Tilia*, and *Ulmus*, and in the younger Jacksonian *Picea*, *Tsuga*, *Acer*(?), *Diospyros*(?), *Fraxinus*(?), and *Nyssa* appear (Frederiksen, 1981, 1988, 1991; Gray, 1960). Although

there are no fossil floras of Paleocene age known from northern Latin America, north-temperate elements are absent from the Eocene Burgas Basin assemblage in northern Mexico (Graham, 1999a; Martinez-Hernandez et al., 1980), the Gatuncillo assemblage in Panama (Graham, 1985), and from early Miocene assemblages in Costa Rica (Graham, 1987) and Panama (Graham, 1988a, b, 1989). These elements are known from a few grains of *Quercus* in the Mio-Pliocene Gatun Formation of Panama, and from a richer assemblage in the middle Pliocene Paraje Solo Formation of southeastern Veracruz, Mexico (*Abies*, *Picea*, *Pinus*, *Alnus*, *Celtis*, *Juglans*, *Liquidambar*, *Myrica*, *Populus*, *Quercus*, and *Ulmus*). Based on this evidence, it appears that the origin of the northern temperate component of the Latin American vegetation was primarily through relatively recent introductions. If north-temperate elements were present prior to the late Miocene, these phantom forests left no substantive record in the fossil assemblages published to date.

Until recently the number of fossil floras by which the models could be evaluated was relatively low. New data from microfossil floras in Chiapas (Mexico), Guatemala, and Costa Rica provide further information on the principal time of origin for north-temperate elements in northern Latin America. The evidence previously discussed would suggest that fossil floras older than about the middle to late Miocene should contain few or no representatives of these elements; rather, they should be present in floras of younger age, and their diversity in the fossil floras should decrease toward the south. The Simojovel flora in Chiapas, Mexico, is Early Miocene in age (Frost & Langenheim, 1974), and it is within the present-day distribution of deciduous trees and shrubs disjunct from eastern North America (Breedlove, 1973; Gómez-Pompa, 1973; Miranda & Sharp, 1950). With the exception of *Pinus*, the fossil flora contains no representatives of eastern deciduous temperate elements (Graham, 1998a, 1999b; Graham & Palacios Chávez, 1996; Langenheim et al., 1967). Temperate habitats were available, but they were occupied by plants such as *Podocarpus* and *Engelhardia*.

In Guatemala, a late Miocene to Mio-Pliocene assemblage of pollen and spores has been recovered from the Padre Miguel-Herrería complex of formations (Graham, 1998a). *Picea*, *Pinus*, *Juglans*, *Quercus*, and *Ulmus* have been identified, revealing a north-temperate component in the late Miocene and Mio-Pliocene that was absent in the older early Miocene Simojovel flora from adjacent Chiapas. Farther south in Costa Rica these elements are absent in the Pliocene Rio Banano Formation (Gra-

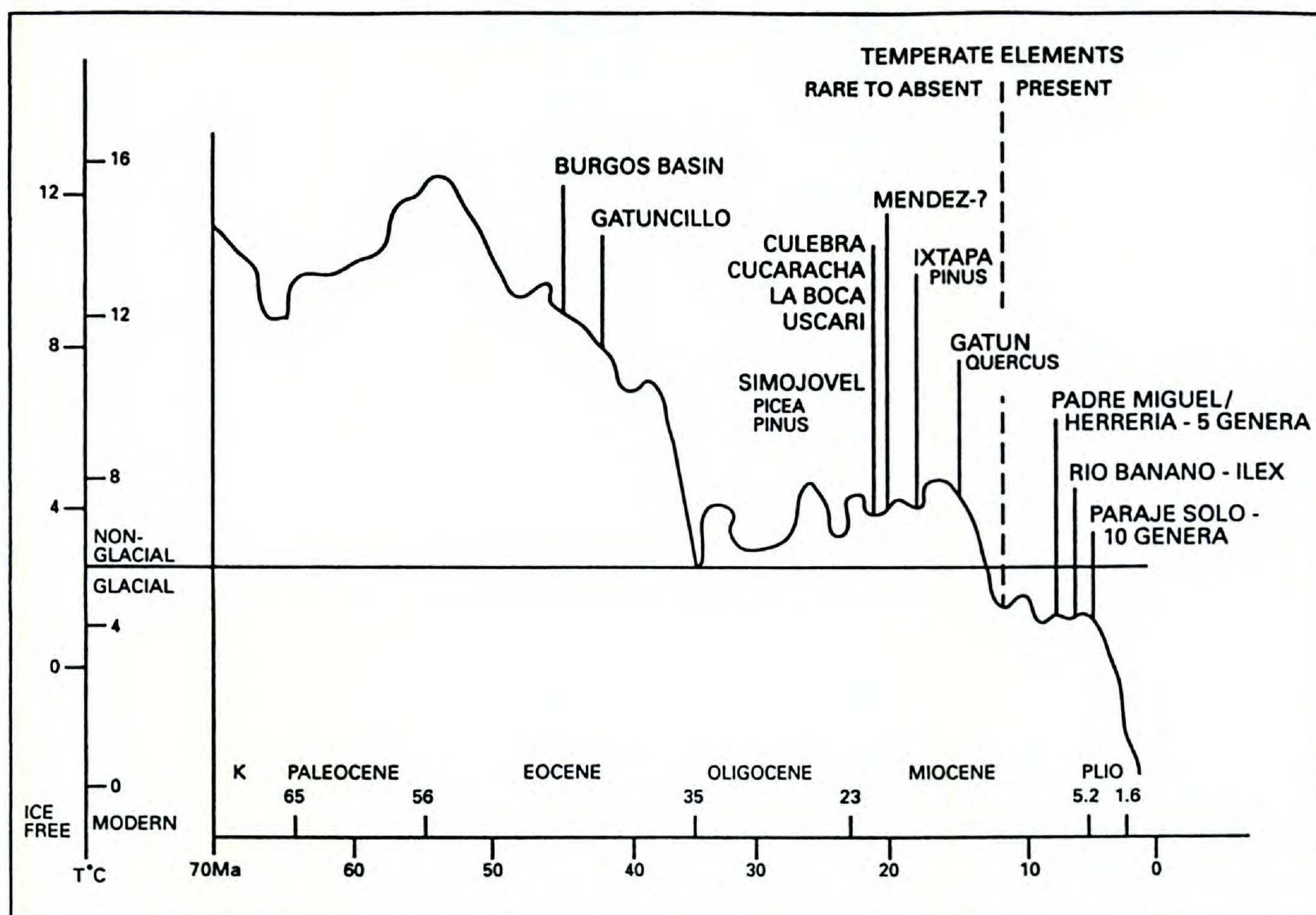


Figure 17. Benthic paleotemperature curve, Tertiary palynofloras from northern Latin America mentioned in the text, and occurrences of northern temperate elements. Paleotemperature curve based on Miller et al. (1987).

ham & Dilcher, 1998). Thus, northern temperate elements are absent from the Eocene Burgos Basin Flora of Mexico, the Eocene Gatuncillo flora of Panama, the early Miocene Simojovel flora of Chiapas, Mexico, the early Miocene Uscari Formation and the Pliocene Rio Banano Formation of Costa Rica, and the early Miocene Culebra, Cucaracha, and La Boca floras of Panama. They are present in Mio-Pliocene floras of Guatemala; in the middle Pliocene Paraje Solo flora of Veracruz, Mexico; and just appear (*Quercus* only) in the Mio-Pliocene Gatun flora of Panama.

The second test is whether these temperate elements appear in northern South America primarily after closure of the Isthmus of Panama (after about the Mio-Pliocene interval). In South America *Salix* appears in the early Pliocene, *Myrica* in the middle Pliocene, *Alnus* at ~1 Ma, and *Quercus* at 330 ka (Hooghiemstra, 1989, 1994; Hooghiemstra & Ran, 1994; Hooghiemstra & Sarmiento, 1991; Wijnga, 1996). One exception may be seeds of *Juglans* reported from presumed Miocene deposits in Ecuador (Brown, 1946), but Manchester (pers. comm. 1997) suggested that radiometric dates are needed to confirm the age of the specimens. *Juglans* may be represented in South America today by as many as five

species (Brako & Zarucchi, 1993; Killeen et al., 1993).

The third test is whether some climatic event occurred at the appropriate time that facilitated the introduction of north-temperate elements into Latin America, and that is evident from an independent line of inquiry. In Figure 17 the floras are plotted on the global benthic paleotemperature curve. A major drop in temperature is evident in the middle Miocene that initiated Antarctic glaciations, expanded continental glaciers on Antarctica, and contributed to the spread of seasonally dry habitats in North America (see discussion in Graham, 1999c, chapters 3 and 7). This drop in temperature is consistent with the timing of the introductions based on the available paleobotanical evidence, and provides a plausible mechanism for the early appearance of the northern temperate component in the neotropical vegetation. Evidence for the slightly later appearance of uplands (Mio-Pliocene) supplementing effects of Late Cenozoic cooling, has been discussed previously (this paper). The pre-existing uplands and rising mountain areas in Central and South America would have been expected to experience more pronounced climate changes than the lowland, coastal areas. It is these upland areas

that likely provided habitats for the early temperate elements.

Origin of the tropical element in the northern Latin American vegetation

New analyses also are providing insights into the origin of the tropical component in northern Latin American vegetation. It has generally been assumed that trees and shrubs in the tropical forests of Mexico and Central America were derived from South America: "Indigenous tropical plants in modern North America are descendants of Tertiary and Quaternary immigrants from South America" (Cronquist, 1988: 153). In general this is true, but it is proving too simplistic.

Wendt (1993) studied the affinities of rainforest canopy trees in Mexico. As expected, the majority of the taxa (75%) are related to ones in South America, and probably arrived via an Isthmian route after formation of the Panama landbridge, and/or by long-distance transport throughout the Cenozoic Era. However, the modern distribution and affinities, and the fossil record of a significant number (~25%), suggest a different history. According to Wendt (1993), modern distributions and relationships indicate that some are of Laurasian origin and probably migrated from the north via the North Atlantic landbridge—*Antirhea*, *Aphananthe*, *Berrya*, *Bourreria*, *Bursera*, *Ehretia*, *Erblichia*, *Federovia*, *Flacourtiaceae* (subtribe *Hydnocarpinae*), *Lonchocarpus*, *Sideroxylon*, *Styphnolobium*, and *Trichospermum*. The fossil record provides evidence for others of Laurasian origin that followed a northern route into Mexico. These are taxa known from the Eocene of the southeastern United States, but which presently have no or only later fossil records in South America—*Celtis*, *Clethra*, *Cordia*, *Ilex*, *Populus*, *Saurauia*, *Salix*, *Talauma*, *Trema*, and *Turpinia*.

A group of African-Gondwanan origin probably arriving from the north includes *Acacia*, *Beilschmiedia*, *Bursera*, *Caesalpinia*, *Cassia*, *Cedrela*, *Chrysophyllum*, *Dalbergia*, *Diospyros*, *Ficus*, *Lonchocarpus*, *Nectandra*, *Ocotea*, *Oreopanax*, *Persea*, *Sabal*, *Sapindus*, *Sapium*, *Sterculia*, and *Terminalia*, while others of Gondwanan origin arriving prior to the landbridge but still via South America may include *Alchornea*, *Allophyllus*, *Apeiba*, *Astronium*, *Bauhinia*, *Bernoullia*, *Casearia*, *Dendropanax*, *Erythrina*, *Eugenia*, *Homalium*, *Luehea*, *Mabea*, *Ochroma*, *Pouteria*, *Tapiria*, *Thouinia*, and *Trichilia*.

The presence of plants of Old World origin in the tropical forests of northern Latin America also has been assessed by a cladistic analysis of two legume

groups (*Dichrostachys* group, tribe Robinieae and allies; Lavin & Luckow, 1993). If a taxon has a modern center of distribution and an early Tertiary fossil record in tropical North America, then there is a high probability that its sister-group will be in the paleotropics and derived relatives will be in South America if it has been introduced from the north from Gondwanan ancestors. The results of the analysis for these legumes supported the hypothesis; namely, the taxa in South America were derived from, and not a source for, the northern tropical ones. In contrast, a similar analysis of the Costa Rican *Ruptiliocarpon* in *Lepidobotryaceae* (Hammel & Zamora, 1993) showed that it is likely an example of the majority of taxa that arrived from South America. The emerging picture is that the tropical forests of northern Latin America, although primarily South American in origin, are more complex than earlier thought and are composed of elements arriving from several sources via different routes and at different times (Graham, 1995; Wendt, 1993).

EVENT IV: QUATERNARY CLIMATE FLUCTUATIONS

The first broad assessment of global Quaternary climates was from the Climate Long-Range Investigation and Mapping Program (CLIMAP) project (CLIMAP Project Members, 1976, 1981, 1984). The resulting model, based on changes in the composition and distribution of planktonic microfossils (e.g., foraminifera), indicated that while high latitudes chilled at glacial maximum at ~ 18 ka, temperatures in the low latitudes remained about the same or to a maximum of about 2° cooler. This is at variance with new oxygen isotope evidence (Guilderson et al., 1994; Schrag, et al., 1996), noble gases dissolved in ¹⁴C-dated ground water (Stute et al., 1995), snow-line depression (Rind & Petet, 1985), continental climate records from pollen analysis, and with global circulation model (GCM) simulations that predict a MAT (mean annual temperature) cooling in the equatorial regions of 5°–6°C at glacial maximum (Colinvaux et al., 1996a, b, and see review in Kerr, 1997). New calcium-strontium ratios from submerged coral reefs (*Acropora palmata*) drilled off the south coast of Barbados (13°N) also favor cooler climates. The element strontium is chemically similar to calcium and can replace calcium in the walls of the corals. The rate of replacement is temperature-sensitive, and measurements indicate temperatures lower by ~ 5°C at ~ 18 ka (Guilderson et al., 1994). Modeling by Webb et al. (1997) demonstrated the mechanism potentially responsible for equatorial cooling.

Other recent data also suggest that the middle and low latitudes responded to fluctuations in Quaternary temperatures (Charles, 1997; Beck et al., 1997; Curry & Oppo, 1997; Webb et al., 1997). A cool interval called the Little Ice Age occurred at ~ 400 years ago and at that time MAT in the Sargasso Sea (~ 32°N) was ~ 1°C cooler than at present. During a warm interval at ~ 1 ka it was ~ 1°C warmer (Keigwin, 1996).

Among the unsettled aspects of Quaternary vegetational history in South America are the history of tropical lowland biotas and the related Haffer model of diversification. Early pollen profiles from the High Plain of Bogotá revealed that treeline fluctuated by ~ 1700 m during the late Pliocene and Quaternary (van der Hammen & Gonzalez, 1960, 1964). This corresponds to a difference in MAT of ~ 8°C at ~ 2500 m; the present MAT is 17–19°C. By extrapolation, a potential lowering of up to ~ 6°C was indicated for the lowlands during the coldest intervals. Glacial climates were also frequently drier because cooler temperatures reduce the rate of evaporation of water from the ocean surface into the atmosphere. In the northern Andes, rainfall was periodically reduced by up to 50% (van Geel & van der Hammen, 1973). The question is whether these changes suggested by geochemical and oxygen isotope data, and evident in the Andean highlands, affected biotas in the lowland Amazon Basin.

Haffer (1969, 1970, 1974, 1982) observed that species diversity among toucans and jaçanas was not uniform across the basin, but was focused at certain locales. These areas of high species diversity corresponded to sites that by their physiography appeared likely to perpetuate moist conditions during periods of aridity (river margins, base of mountain slopes). The model envisioned rainforest biota concentrated in refugia during cooler/drier glacial cycles, while drier forest and savanna-like vegetation occupied the intervening area. During warmer/moister interglacial cycles, the rainforest expanded from these sites and coalesced, while the drier communities either persisted on edaphically dry tablelands with sandstone substrata in the lowlands, or occupied the surrounding slopes, as at present. The periodic fragmentation and reuniting of ranges facilitated speciation by allopatry and hybridization, and was proposed as one mechanism accounting for the high diversity of the lowland tropical biota. Several other lines of evidence were interpreted as supporting the model, including the presence of stone lines which form under arid conditions, and the concentration of plant and insect species at sites identified as refugia on the basis of bird distribution (see papers in Prance, 1982).

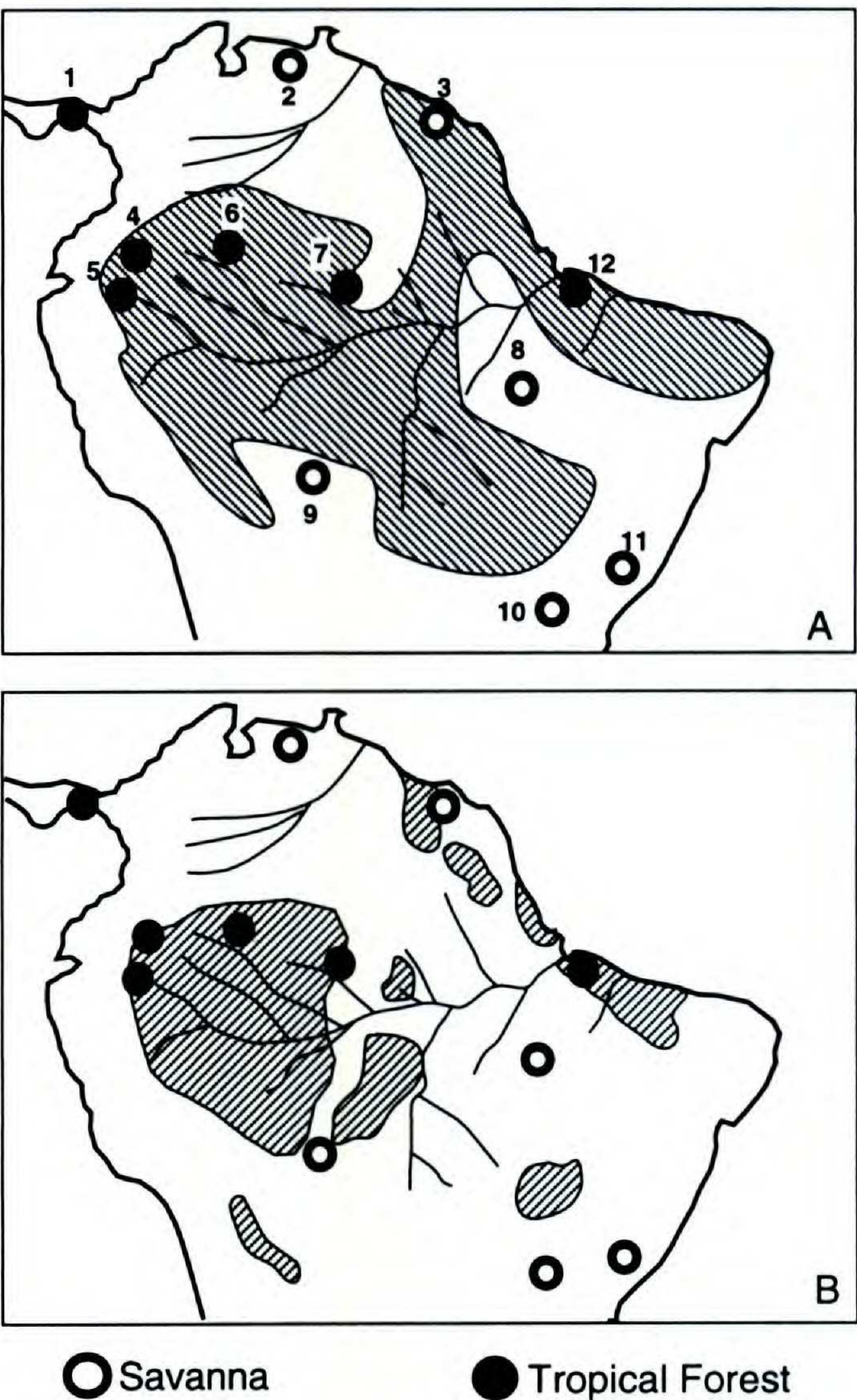


Figure 18. Projected rainforest distribution in Amazonia during the Pleistocene, with (A) 25% and (B) 40% reductions in rainfall from present-day values. Shaded area shows rainfall over 1500 mm annually. Palynological samples from Amazonia shown by symbols, with interpreted vegetation indicated by symbol coding. After Absy and van der Hammen, 1994; Colinvaux, 1996; Behling, 1998. Sites are (informal names): 1, La Yeguada; 2, Lake Valencia; 3, Guianas; 4, Mera; 5, San Juan Bosco; 6, Caqueta River; 7, Lake Pata; 8, Carajas; 9, Katira (Rondonia); 10, Lagoa Campestre; 11, Catas Altas; 12, Lagoa Curuça.

Lacking was paleobotanical information directly from the lowland Amazon Basin, and ancillary information on neotropical Quaternary environments derived from independent lines of inquiry. New data were recently published for lower-elevation sites around the Amazon Basin and for other locations in the lowlands (Fig. 18). Considering the immense complexity of the tropical ecosystem, and the difficulties and limitations inherent in trying to reconstruct its past, it is not surprising that a consensus has not yet been achieved. Only a few plant-bearing sites that extend into the last glacial interval (older than ~ 12 ka) have been published. Haberle (1997) reported data from Amazon fan

cores spanning 160,000 years that show percentages of grass and shrub pollen less than or equal to 25%, a value interpreted as indicating limited savanna development in the Amazon basin. As noted by Haberle (Haberle, 1997; see also Kerr, 1996), a few hundred sites in the Amazon Basin may be necessary to get a clear picture of environmental change and biotic response. In assessing the present information it is also necessary to distinguish between evidence for cool temperatures and for aridity. There is a broad association between warm-moist climates and tropical vegetation in the lowlands during the interglacials (as at present), and cool-dry climates and drier forest/more open savanna-like vegetation during glacial times. It has been suggested, however, that significant cooling occurred in the lowlands of Amazonia without the accompanying dryness that would have converted areas occupied by rainforest to savanna (Colinvaux, 1996). There are insufficient data for dogmatic conclusions about Quaternary environments in the Amazon, and an even-handed review must include much that is a matter of opinion.

Along the eastern slopes of the Andes at Mera (~ 1°S; 1100 m elevation) and San Juan Bosco (~ 3°S; 900 m elevation) in Ecuador, pollen profiles show that the upper range of temperature-sensitive plant populations was lower by ~ 700 m between 33,500 and 26,500 yr B.P. (late middle Glacial) and that elements from the uplands intermingled with lowland forest communities. This implies a MAT lower by ~ 4°C (earlier estimates) to 7–9°C (more recent estimates; Bush et al., 1990; Colinvaux, 1996; Colinvaux & Liu, 1987; Liu & Colinvaux, 1985) and a moist rainfall regime. However, the sites are near the base of the eastern Andes where the present annual rainfall is ~ 5 m. This physical setting qualifies as a potential refugium that would have remained moist during dry intervals.

At Lake Pata in northwestern Brazil (0°N; 300 m elevation) the pollen record extends back to ~ 42 ka. Throughout the profile, tree pollen constitutes 70–90% of the assemblage, while herb pollen remains below 10%. Pollen from trees that now grow mostly 800–1000 m above the Pata site were present (*Podocarpus*, 10%; associated *Ericaceae*, *Hedyosmum*, *Humiria*, *Ilex*, *Melastomataceae*, *Rapanea*, *Weinmannia*) at glacial maximum, and this was interpreted to mean a MAT 5–6°C lower than at present (Colinvaux et al., 1996a, b). The inference is that at glacial maximum the area was forested, and was not occupied by savanna. Also, if the area was sufficiently moist throughout the past ~ 42 ka to support forest, even though 5–6°C cooler, this supports the contention that lower temper-

atures prevailed throughout the lowlands without appreciable dryness. One complication is that on the basis of meteorological evidence, the area of Lake Pata also has been considered a refugium, and by the Haffer model it would be expected to support forest during dry intervals (van der Hammen & Absy, 1994). In addition, large reproductive stands of *Podocarpus* are found at sea level in Central America, on both the Atlantic and Pacific Coasts, which throw into question the use of this genus as an exclusively cooler-climate indicator.

Data from other sites suggest that a patchwork of vegetation may have existed in the lowlands at the coldest intervals which included moist forests and drier communities. At Carajás (southeastern Amazonia, Brazil; 6°S), pollen profiles reflect changes in vegetation for the last 60 ka (Absy et al., 1991). The site is on a table mountain at 700–800 m elevation, today covered with forest and edaphic savanna, and surrounded by Amazonian forest. The pollen diagrams were interpreted as showing that wet intervals (forest on the hills and in the lowlands; lake levels high) alternated with drier intervals (expansion of savanna on the hills and in the lowlands; lake levels low). At Rondônia, Brazil (9°S) in lowland Amazonia, the sequence is from primarily rainforest (interglacial), to savanna (glacial; 42,500 ± 2,500 to 18,500 yr B.P.), to modern rainforest after ~ 11 ka (Absy, 1979; Absy & van der Hammen, 1976; van der Hammen, 1972). Geomorphic and pollen data from the middle Caquetá River area in Colombia and eastern Peru also are interpreted to show that local vegetation alternated between Amazonian forest and more open caatinga (van der Hammen et al., 1992a, b).

In the “Lagoa Campestre” (Lake) of Salitre in southern Brazil (19°S; 970 m elevation), pollen diagrams show an arid phase between ~ 50 and 40 ka (Ledru et al., 1996). This interval is characterized by low frequencies of arboreal pollen (0.5–3%). *Asteraceae* (18.5–28%) and *Poaceae* (69–70%) are dominant among the non-arboreal taxa. This pollen assemblage is poor in taxa and indicates open, treeless vegetation surrounding a shallow pond with no fringe of aquatic vegetation. The low frequency of arboreal taxa indicates that trees were growing only at a distance. This suggests the presence of landscapes found today in central and northern Argentina, where the climate is cool and dry (Ledru et al., 1996). Other areas where reduced rainfall (~ 10–20%) and dry vegetation replaces forest in the Quaternary include the Guianas (Wijmstra & van der Hammen, 1966; Salgado-Labouriau, 1980) and the Galápagos Islands (Colinvaux, 1972), as well as East Africa (Livingstone,

1975). In an extensive review of the geology and geomorphology of South America, Clapperton (1993a: 162) concluded, "The important message is that climatic conditions appear to have fluctuated between humid and dry, and as the present interglacial climate is humid, it seems reasonable to assume that dry intervals corresponded to periods of global glaciation."

A study of ice cores from Huascarán in the north-central Andes of Peru ($\sim 9^\circ\text{S}$, 6000 m elevation) has revealed Quaternary climatic fluctuations back 20 ka that parallel those from the North Atlantic (Thompson et al., 1995). Oxygen isotope ratios show that between 20 ka and 14.5 ka temperatures at this elevation were $8\text{--}12^\circ\text{C}$ cooler than at present. This would be consistent with the $\sim 6^\circ\text{C}$ lowering of temperatures estimated for the lowlands. In addition, there was a 200-fold increase in dust and lower nitrate levels in the cores. Thompson and co-authors (1995: 47) concluded, "The extreme dustiness of the LGS [late glacial stage] ice on Huascarán is consistent with reconstructions [Clapperton, 1993b; van der Hammen & Absy, 1994] for South America that indicate a reduction in atmospheric humidity, precipitation, and forest and grass cover during the LGS along with an enhancement of eolian deposits such as dune fields and deflation basins [Clapperton, 1993a], because winds were stronger and surface conditions were drier." With reference to the low nitrate levels, Thompson et al. (1995: 47) further noted they "may imply that forest cover was significantly reduced in response to dry conditions and the expansion of grassland, as suggested by palynological studies in Brazil [Clapperton, 1993b]."

To the north, the history of Quaternary vegetation in lowland Panama is preserved in sediments from El Valle (500 m elevation; $> 30,700 \pm 800$ to $8,350 \pm 150$ yr B.P.) and Lake La Yeguada (650 m; 14 ka to the present). These records have been interpreted to indicate lowland representation of taxa currently found at elevations ~ 800 m higher (Bush & Colinvaux, 1990; Bush et al., 1992). The MAT is estimated at $4\text{--}6^\circ\text{C}$ cooler, but still moist, and the vegetation as remaining forested throughout the sections. In the Petén of Guatemala, the temperature depression is estimated at $\sim 8^\circ\text{C}$ cooler in the late Quaternary (Leyden, 1984; Leyden et al., 1993), but Leyden also emphasized increased aridity at interglacial-glacial transitions.

In addition to temperature and precipitation, another factor affecting lowland tropical biotas is sea-level change associated with glacial history. A recent estimate is for a lowering of $\sim 121 \pm 5$ m at glacial maximum (Geophysics Study Committee,

1990). Considering that much of the Amazon Basin is near sea level, a change of this magnitude must have had some drying effect on vegetation through fluctuations in water table.

There are a number of indications that late Glacial and early Holocene climates in the neotropical lowlands included cooler and drier intervals, and variously supported a mosaic of moist forests and drier forests to savanna-like vegetation. These are: (1) fossil mammalian faunas in Central and South America (Webb & Rancy, 1996), (2) a trend toward drier conditions and a more complex array of communities developing near the end of the Tertiary Period in Costa Rica and Panama (Graham, 1992); (3) aridity at interglacial-glacial transitions in Guatemala (Leyden, 1984; Leyden et al., 1993); (4) geomorphic features suggesting aridity during the Quaternary in the Amazon lowlands (Ab'Sáber, 1982; Clapperton, 1993a); (5) marked changes in sea level (Geophysics Study Committee, 1990); and (6) Quaternary aridity demonstrated from other adjacent and distant parts of the world (the Guianas, Wijmstra & van der Hammen, 1966; Galápagos Islands, Colinvaux, 1972; Lake Valencia, Venezuela, Leyden, 1985; East Africa, Livingstone, 1975). This evidence is open to other interpretations: either that the lower rainfall was insufficient to cause forest to be replaced by dry-forest or savanna, or that such replacements were localized (Colinvaux, 1996).

The consensus developing is that late Tertiary and Quaternary sea level and climatic fluctuations affected the lowland biotas of the Neotropics, and that the magnitude of the temperature change was $\sim 6^\circ\text{C}$. There is less agreement about aridity and the closed forest versus more open forest or savanna-like nature of the vegetation. Colinvaux (1996) has emphasized cooler climates, sustained moisture, and forested vegetation throughout much of the late Quaternary. This would negate any significant role for refugia-like mechanisms in accounting for the high level of diversity in neotropical biotas. In contrast, other authors see evidence for periods of aridity and open vegetation in the pollen profiles and from other kinds of data. Revisions may become necessary in the proposed locations, extent, and patterns of some forest refugia and savannas in the Amazonian lowlands as envisioned in the original Haffer model. It is further true that climate-induced refugial events in the Quaternary Period were not the only mechanisms influencing rainforest diversity. Recently, it has been discovered that the modern distributions of some lineages of rodents and marsupials in the Amazon Basin conform not to the present barriers formed by river

drainage systems, but to ancient ridges that divide the basin into sub-basins (Patton & da Silva, 1998; summary by Morell, 1996). These ridges formed when the Andes were uplifted $\sim 2\text{--}5$ Ma and divided the range of some species into reproductively isolated subsets that are still detectable by mtDNA analysis. Subsequent erosion and basin filling have nearly obliterated these Pliocene barriers. They suggest changes in the physical landscape are another mechanism generating neotropical species diversity. Nonetheless, the combination of temperatures $\sim 6^\circ\text{C}$ cooler, sea level ~ 120 m lower, and pollen sequences indicating at least locally dry habitats and open vegetation are compelling. They create a view of lowland neotropical vegetation alternating between closed forest and more dry open forest or savanna-like vegetation during the environmental fluctuations of the late Tertiary and Quaternary Period.

Our concept of the pace of these fluctuations has also undergone substantial renovation. The older view of four major glacial advances each lasting ~ 175 ka, separated by three interglacials of about equal duration, has been replaced by a model depicting 18–20 cycles within the past 1.6 Ma and 9 within the past 800 ka [Davis, 1983; Johnson, 1982; Greenland Ice-core Project (GRIP) Members, 1993], and shorter ones on the order of several hundred (Dansgaard-Oeschger or D-O events) to several thousand years duration (Heinrich events). Whatever the disruptions of neotropical vegetation from temperature, precipitation, physical, and sea-level changes, they were taking place at a much more rapid pace than previously envisioned. Thus, the older concept of stable and unchanging tropical vegetation has given way to one of a dynamic, ephemeral, and delicately balanced assemblage.

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Appendix 1. Published plant fossil localities ranging geographically from Costa Rica to Bolivia, and temporally from Late Cretaceous to Quaternary Periods. Localities are sorted by country, and within country by geologic age and then ordered alphabetically by author of the work. When several countries are treated by a single publication, the publication is listed under the first country in alphabetical order.

Country	Geological age	Author(s)	Date of publica- tion	Local place name	Organs studied
Bolivia	Pliocene	Berry	1939a	Potosi	leaves
Bolivia	Pliocene	Berry	1917	Potosi & Corocoro	leaves & fruits
Bolivia	Mio-Pliocene	Berry	1940	Agua Salada	fruit
Bolivia	Mio-Miocene	Berry	1922a	Pisllypampa	fruits
Bolivia	Miocene	Berry	1922b	Jancocata	leaves
Bolivia	Miocene	Britton	1892	Potosi	leaves
Bolivia	Miocene	Engelhardt	1888	Cerro de Potosi	leaves
Bolivia	Miocene	Engelhardt	1894	Potosi	leaves
Bolivia	Miocene	Gregory et al.	1998	Jakokkota (=Jancocata)	leaves
Bolivia	Miocene	Singewald & Berry	1922	Corocoro	leaves
Br. Guiana/ Suriname	Paleocene to Mio- cene	Van der Hammen & Wymstra	1964		pollen
Brazil	Quaternary	Absy	1985		pollen
Brazil	Quaternary	Absy & van der Hammen	1976	Rondonia, Katira, Capoeira & Rio Preto	pollen
Brazil	Quaternary	Absy et al.	1991	Serra dos Carajas	pollen
Brazil	Quaternary	Behling	1995	Lagoa do Pires	pollen
Brazil	Quaternary	Behling	1996	Lagoa de Curuca	pollen
Brazil	Quaternary	Behling	1998	Morro de Itapeva, SP	pollen
Brazil	Quaternary	Behling	1998	Cata Altas	pollen
Brazil	Quaternary	Behling & Hooghiem- stra	1998	Laguna Angel & Laguna Sardinas	pollen
Brazil	Quaternary	Colinvaux et al.	1996a	Lake Pata—Hill of Six Lakes	pollen
Brazil	Quaternary	DeOliveira	1992		pollen
Brazil	Quaternary	Duarte & Nogueira	1985	Morro do Chapau, Bahia	leaves
Brazil	Quaternary	Duarte & Vasconcelos	1980	Umbuzerio	leaves
Brazil	Holocene	Ledru	1992	Lake Carajas & Lake Salitre	pollen
Brazil	Quaternary	Salgado-Labouriau et al.	1997	Goias, Crominia	pollen
Brazil	Pliocene	Berry	1935a	Bahia & Minas Gerais	leaves
Brazil	Pliocene	Berry	1937d	Acre	leaves
Brazil	Pliocene	Bonnet	1905	Bahia	leaves
Brazil	Pliocene	Dolianiti	1949	Minas Gerais, Fonseca	leaves
Brazil	Pliocene	Dolianiti	1950	Minas Gerais, Fonseca	leaves
Brazil	Pliocene	Hollick & Berry	1924	Bahia	leaves
Brazil	Pliocene	Krasser	1903	Ouricanga, Alagoihas, Bahia	leaves
Brazil	Pliocene?	Selling	1945	Bahia	fruit
Brazil	Miocene	De Lima & Angulo	1990	Alexandra Formation near Curitiba, Parana	pollen
Brazil	Miocene?	Duarte	1972	Pirabas, Para	leaves
Brazil	Miocene	Hoorn	1993	Solimoas Formation	pollen
Brazil	Miocene	Mandarim-de-Lacerda	1992	Taubate Basin	leaves
Brazil	Oligocene	De Lima et al.	1985	Sao Paulo	pollen
Brazil	Eocene-Oligocene	Martins-Neto	1989	Taubate Basin	leaves
Brazil	Eocene-Oligocene	Beurlen & Sommer	1954	Rio de Janeiro	leaves & fruit
Brazil	Oligo-Eocene	De Lima & Salard- Cheboldaeff	1981	Gandarela & Fonseca, Minas Gerais	pollen

Appendix 1. Continued.					
Country	Geological age	Author(s)	Date of publication	Local place name	Organs studied
Brazil	Eocene	De Lima, Junior & Stefani	1996	Macacu-Rifte de Guanabara	pollen
Brazil	Tertiary	Dolianiti	1955	Recife	fruits
Brazil	Eocene-Oligocene	Duarte & Rezende-Martins	1983	Vargem Grande do Sul	leaves & fruits
Brazil	Eocene-Oligocene	Duarte & Rezende-Martins	1985	Vargem Grande do Sul	leaves
Brazil	Eocene	Fittipaldi et al.	1987	Bacia de São Paulo	leaves
Brazil	Cretaceous	Crane & Maisey	1991	Santana	pollen
Brazil	Cretaceous	Duarte	1985	Santana	leaves
Brazil	Aptian	Duarte & Silva-Santos	1993	Maranhão	leaves
Brazil	Cretaceous	Herngreen	1975	Alagoas	pollen
Brazil	Cretaceous	Osborn et al.	1993	Santana (NE Brazil)	pollen
Brazil	Cretaceous	Pons et al.	1992	Pernambuco	fruits & leaves
Brazil & Guyana	Quaternary	Van der Hammen & Absy	1994	Rondonia & Carajas	pollen
Brazil, Ecuador, Colombia	Tertiary	Langenheim & Beck	1968	Capanema & Para	ambers
Colombia	Pleistocene	Bakker et al.	1989	Pitalito Basin	pollen
Colombia	Quaternary	Behling et al.	1999	Pantano de Monica	pollen
Colombia	Quaternary	Gonzalez et al.	1965	Sierra Nevada del Cocuy	pollen
Colombia	Quaternary	Helmens & Kuhry	1986	Paramo de Agua Blanca	pollen
Colombia	Quaternary	Hooghiemstra & Ran	1994		pollen
Colombia	Quaternary	Hooghiemstra & Van der Hammen	1993	Cundinamarca	pollen
Colombia	Holocene	Van der Hammen & Gonzalez	1960	Eastern Cordillera: Laguna de La América	pollen
Colombia	Quaternary	Van der Hammen & Gonzalez	1960	Sabana de Bogotá: Palacio A	pollen
Colombia	Quaternary	Van der Hammen & Gonzalez	1965	Boyaca	pollen
Colombia	Pliocene-Present	Andriessen et al.	1993	Eastern Cordillera	pollen & sediments
Colombia	Pliocene	Boureau & Salard	1962	Bolívar	wood
Colombia	Pliocene-Present	Hooghiemstra	1994	Eastern Cordillera	pollen
Colombia	Pliocene-Present	Hooghiemstra & Sarmiento	1991	Bogotá	pollen
Colombia	Pliocene	Howe	1974	Magdalena Valley	leaves
Colombia	Pliocene	Solé de Porta	1960	Cerro de la Popa, Cartagena	pollen
Colombia	Pliocene-Present	Van der Hammen & Hooghiemstra	1997	High Plain of Bogotá	pollen
Colombia	Pliocene-Present	Van der Hammen et al.	1973	Sabana de Bogotá	pollen
Colombia	Pliocene	Wijninga	1996a	Cordillera Oriental	pollen, leaves, wood, seeds
Colombia	Pliocene	Wijninga	1996b	High Plain	pollen, seeds, fruits, wood, leaves
Colombia	Pliocene	Wijninga & Kuhry	1990	Subachoque Valley	pollen & leaves
Colombia	Pliocene	Wijninga & Kuhry	1993	Guasca Valley	pollen & leaves
Colombia	Miocene	Berry	1936b	Santander	leaves

Appendix 1. Continued.					
Country	Geological age	Author(s)	Date of publication	Local place name	Organs studied
Colombia	Mio-Pliocene	Berry	1945b	East of Cordillera de Bogotá	leaves
Colombia	Miocene	Hoorn	1994a	Caqueta River	pollen
Colombia	Oligocene through Pliocene probably	Mirioni	1965	Amaga, Prov. Bolívar, Magdalena Valley	wood
Colombia	Miocene or Pliocene	Pons	1965	Tolima Province	leaves
Colombia	Miocene	Pons	1969	Magdalena Valley	wood
Colombia	Miocene	Pons	1976	Tolima	leaves
Colombia	“Late Tertiary”	Pons	1979	Hato Grande, Tolima	leaves
Colombia	Miocene	Pons	1985	Magdalena Valley	leaves
Colombia	Miocene	Solé de Porta	1963	Cira del Valle Formation, Magdalena Valley	pollen
Colombia	Miocene	Wijninga	1996b	Tequendama	pollen, leaves, wood, fruits
Colombia	Oligocene-Miocene	Duenas	1977	Planeta Rica	pollen
Colombia	late Eocene or Oligocene	Berry	1924a	Cundinamarca	fruits
Colombia	Oligocene	Berry	1925b	East of Bogotá	seeds
Colombia	Oligocene	De Porta & Solé de Porta	1962	Magdalena Valley	pollen
Colombia	Oligocene & Miocene	Hoorn	1988	Araracura	pollen
Colombia	Oligocene	Marty	1933	near Yurumangui & Naya	leaves
Colombia	Oligo-Miocene	Pons	1983	Planeta Rica	seed
Colombia	Oligo-Miocene	Solé de Porta	1961a, b	Magdalena Valley, Santander	pollen
Colombia	Oligocene and Eocene	Berry	1924a	Cundinamarca & Bolívar	fruits & seeds
Colombia	Oligocene	Reid	1933	near Yurumangui & Naya	fruits
Colombia	Eocene, Miocene	Berry	1929c	Bolívar; Cundinamarca; Boyaca	leaves
Colombia	Paleocene-Eocene	Doubinger & Pons	1970	Magdalena Valley	leaves & fungi
Colombia	Eocene	Gonzalez-Guzman	1967	Tibu	pollen
Colombia	Eocene	Huertas	1977	near Medellin	leaves
Colombia	Eocene-Oligocene	Schuler & Doubinger	1970	D’Amaga	pollen
Colombia	Tertiary	Solé de Porta	1961b	near Monteria & Planeta Rica	pollen
Colombia	Eocene-Oligocene	Van der Hammen & Garcia de Mutis	1966		pollen
Colombia	Paleocene	Van der Kaars	1983	Guajira Province	pollen
Colombia	Paleogene	Doubinger & Pons	1970	Guajira	cuticle
Colombia	Cretaceous	Huertas	1960	Sabana de Bogotá, Zipaquirá	leaves
Colombia	Cretaceous	Huertas	1969	Cundinamarca	fruit
Colombia	Cretaceous	Huertas & Van der Hammen	1953	Villeta	fruit
Colombia	Cretaceous	Stough	1968	Sabana de Bogotá	pollen
Colombia	Cretaceous through lower Tertiary	Van der Hammen	1954	High Plain of Bogotá	pollen
Colombia & Guyana	Quaternary	Wijmstra & Van der Hammen	1966	Laguna Agua Sucia-Rupununi	pollen
Colombia, Brazil, Peru	Miocene	Hoorn	1994b	Pebas, Solimoes	pollen

Appendix 1. Continued.

Country	Geological age	Author(s)	Date of publica- tion	Local place name	Organs studied
Colombia	Miocene	Hoorn & Lorente	1992	Caqueta River	pollen
Costa Rica	Quaternary	Hooghiemstra et al.	1992	Talamanca	pollen
Costa Rica	Pliocene	Graham & Dilcher	1998	Río Banano near Zent	pollen
Costa Rica	Miocene	Berry	1921a	Talamanca Valley	leaves
Costa Rica	Miocene	Graham	1987	Uscari	pollen
Ecuador	Quaternary	Bush & Colinvaux	1988	Lake Ayauch	pollen
Ecuador	Pleistocene	Bush et al.	1990	Mera, San Juan Bosco	pollen, phyto- liths
Ecuador	Pleistocene	Heine	1994	Mera	pollen, radiocar- bon
Ecuador	Pleistocene	Liu & Colinvaux	1985	Mera	pollen, wood
Ecuador	Miocene	Berry	1929a	Loja	leaves
Ecuador	Miocene	Berry	1933	Loja Basin	fern
Ecuador	Miocene	Berry	1934a	Cuenca Basin	leaves
Ecuador	Miocene	Berry	1935b	Malacatos	leaves
Ecuador	Miocene	Berry	1945a	Loja Basin	leaves
Ecuador	Mio-Pliocene	Brown	1946	Esmeraldas	seeds
Ecuador	Mio-Pliocene	Brown	1956	Punta Gorda	seeds
Ecuador	Miocene	Burnham	1955a, b	Loja	fruit
Ecuador	Miocene	Wolf & vom Rath	1876	Loja	leaves
Ecuador	Eocene	Berry	1929d	Santa Elena	fruits
Ecuador	Eocene	Berry	1932	Santa Elena	fruits
Ecuador	Cretaceous	Shoemaker	1982	El Oro	leaves & wood
Ecuador & Colombia	Miocene	Engelhardt	1895	Loja & Santa Ana	leaves
Guyana	Paleocene-Eocene	Leidelmeyer	1966	near Georgetown, Mom- baka	pollen
Panama	Quaternary	Bush & Colinvaux	1990	El Valle	pollen
Panama	Quaternary	Bush & Colinvaux	1994	Darien—Lake Wode- house	pollen
Panama	Pleistocene	Bush et al.	1992	Veraguas Province	pollen, phyto- liths
Panama	Oligocene	Berry	1918	Canal Zone	leaves & wood
Panama	Miocene	Berry	1921b	Canal Zone	nut
Panama	Eocene	Graham	1985	Alcalde Díaz	pollen
Peru	Quaternary	Hansen et al.	1994	Andean	pollen
Peru	Miocene	Berry	1920a	Tumbes	leaves
Peru	Pliocene	Berry	1923	Cajamarca	leaves
Peru	Pliocene?	Berry	1925a	Loreto	leaves
Peru	Miocene	Cruzado-Casteneda & Celi-Navarrete	1985	Tumbes Province	pollen
Peru	Miocene	Wood et al.	1992	Tumbes	pollen
Peru	Oligocene	Berry	1924b	Parinas Point, Piura	fruits
Peru	Eocene	Berry	1929b	Belen	fruits & seeds
Peru	Oligocene	Berry	1934b	Chira Valley	seeds
Peru	Eocene	Berry	1937e	Piura	leaves
Peru	Cretaceous	Mourier et al.	1988	Morerilla	wood
Peru/Ecuador	Pleistocene/Holo- cene	Hansen & Rodbell	1995	Laguna Baja	pollen
Puerto Rico	Oligocene	Graham	1996	San Sebastian	pollen, leaves
Trinidad	Miocene	Berry	1925c	Siparia & Moruga	leaves
Trinidad	Miocene	Berry	1937a	Forest Reserve, Fyzabad	leaves
Trinidad	Mio-Pliocene	Berry	1937b	Mud Plant Forest Re- serve	leaves

Appendix 1. Continued.

Country	Geological age	Author(s)	Date of publica- tion	Local place name	Organs studied
Venezuela	Quaternary	Leyden	1985	Lake Valencia	pollen
Venezuela	Holocene	Rinaldi et al.	1990	Gran Sabana	pollen
Venezuela	Holocene	Rull	1987	Venezuelan Andes	pollen
Venezuela	Holocene	Rull	1991	Guaiquinima, Chimanta & Auyan	pollen
Venezuela	Holocene	Rull	1992	Gran Sabana	pollen
Venezuela	Holocene	Rull	1996a	Pantepui Province	pollen
Venezuela	Pleistocene-Recent	Rull	1996b	Lake Valencia	pollen
Venezuela	Pleistocene	Rull	1998b	Mesa de Caballo	pollen
Venezuela	Holocene	Rull & Vegas-Vilarru- bia	1993	Carinapay	pollen
Venezuela	Holocene	Rull et al.	1987	Piedras Blancas	pollen
Venezuela	Pleistocene	Salgado-Labouriau	1987	Piedras Blancas	pollen
Venezuela	Quaternary	Salgado-Labouriau	1991	Merida Andes	pollen
Venezuela	Pleistocene	Schubert & Rull	1988	Auyan tepui	pollen
Venezuela	Miocene	Berry	1920b	near Lake Maracaibo	seed
Venezuela	Miocene	Berry	1921c	Trujillo	leaves
Venezuela	Miocene	Berry	1937c	Falcon	leaves & fruit
Venezuela	Pliocene?	Berry	1939b	Anzoategui	leaves
Venezuela	Miocene	Hambalek et al.	1994	Urumaco trough	pollen
Venezuela	Miocene	Hoffman	1931	Betijoque	leaves
Venezuela	Eocene and Mio- cene	Berry	1936a	Trujillo; Zulia; Falcon;	leaves
Venezuela	Eocene	Berry	1939b	Maracaibo Basin	leaves
Venezuela	Eocene	Colmenares & Teran	1993	Maracaibo Basin	pollen
Venezuela	Eocene	De Di Giacomo & Van Erve	1987	Falcon	pollen
Venezuela	Eocene	Norem	1955	Maracaibo Basin	pollen
Venezuela	Eocene	Rull	1998a	Misoa Formation	pollen
West Indies	Miocene	Hollick	1924	all islands of the West Indies mentioned sep- arately	leaves

Appendix 2. Comparison of principal palynomorphs from Quaternary deposits in southern Central America and northern South America. Numbers refer to the following references: 1 = Bartlett & Barghoorn, 1973; 2 = Bush & Colinvaux, 1988; 3 = Bush & Colinvaux, 1990; 4 = Bush et al., 1990; 5 = Colinvaux, 1996; 6 = Hooghiemstra, 1984 (table 2); 7 = Hooghiemstra et al., 1992; 8 = Hooghiemstra & van der Hammen, 1993; 9 = Horn, 1985; 10 = Liu & Colinvaux, 1988; 11 = Martin, 1961; 12 = van der Hammen & Absy, 1994. Cheno-Am = Chenopodiaceae-Amaranthaceae undifferentiated; ERA = Euphorbiaceae-Rutaceae-Anacardiaceae undifferentiated. Taxa are presented in the following order: ferns and fern allies, gymnosperms, monocots, and dicots.

Taxon	Lowland Central America	Upland Central America	Lowland South America	Upland South America
<i>Acrostichum</i> 1	x			
<i>Cnemidaria</i> 1, 7, 9	x	x		
<i>Ctenitis</i> 1	x			
Cyatheaceae: <i>Cyathea</i> 1, 3, 6, 7, 8, 9, 11	x	x	x	x
<i>Danaea</i> -type 1	x			
<i>Elaphoglossum</i> 7		x		
Hymenophyllaceae: <i>Hymenophyllum</i> 7, 9	x	x		
<i>Isöetes</i> 7, 8, 11, 12		x	x	x
<i>Jamesonia</i> 7		x		
<i>Lophosoria</i> 7		x		
<i>Lycopodium</i> 1, 7, 8, 11	x	x		x
Monolete fern spore 1, 3, 4, 7, 8, 9, 10, 12	x	x	x	x
Ophioglossaceae 7, 9	x	x		
<i>Pteris</i> 9	x			
Trilete fern spore 1, 4, 5, 8, 9, 10, 12	x		x	x
<i>Selaginella</i> 1	x			
<i>Araucaria</i> 5			x	
<i>Pinus</i> 9	x			
<i>Podocarpus</i> 1, 4, 5, 6, 7, 8, 9, 10, 11, 12	x	x	x	x
Cyperaceae 1, 2, 3, 4, 5, 7, 8, 9, 10, 11, 12	x	x	x	x
<i>Eichhornia</i> 12			x	
Eriocaulaceae 7		x		
Gramineae 1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12	x	x	x	x
<i>Iriarte</i> 1	x		x	
<i>Iriarte</i> -type 9	x			
Liliaceae 9	x		x	
<i>Mauritia</i> 5, 10, 12			x	
Palmae 2, 4, 5, 7, 9, 10, 12	x	x	x	
<i>Phytelephas</i> 1	x			
<i>Potamogeton</i> 8				x
<i>Sagittaria</i> 12			x	
<i>Typha</i> 1, 3, 7, 9	x	x		
<i>Abutilon</i> -type 9	x			
<i>Acalypha</i> 1, 2, 6, 7, 8, 9, 10, 12	x	x	x	x
<i>Alchornea</i> 1, 2, 4, 5, 6, 7, 8, 9, 10, 12	x	x	x	x
<i>Alnus</i> 1, 4, 5, 6, 7, 8, 9, 11	x	x	x	x
<i>Alfaroa</i> / <i>Oreomunnea</i> 7, 9, 11	x	x		
<i>Alternanthera</i> 3, 5, 9	x		x	
<i>Ambrosia</i> -type 10			x	
Anacardiaceae 1, 8, 9	x			x
<i>Anacardium</i> -type 9	x			
Annonaceae 1	x			
<i>Antidaphne</i> 7		x		
<i>Apeiba</i> 1, 9	x			
<i>Aphelandra</i> 1, 9	x			
Apocynaceae 1, 12	x		x	

Appendix 2. Continued.

Taxon	Lowland Central America	Upland Central America	Lowland South America	Upland South America
<i>Avicennia</i> 1, 9	x			
<i>Bauhinia emarginata</i> 1	x			
<i>Billia colombiana</i> 6, 8				x
<i>Bocconia</i> 6, 8				x
Bombacaceae: <i>Bombacopsis</i> 1, 12	x		x	
<i>Borreria</i> 1, 8	x			x
<i>Bravaisia</i> 9	x			
<i>Brunellia</i> 6, 8				x
<i>Byttneria</i> 1	x			
<i>Bursera</i> 1, 5, 9	x		x	
<i>Byrsonima</i> 1, 3, 5, 9, 10	x		x	
<i>Calliandra</i> 1	x			
<i>Canavalia</i> 1	x			
<i>Cardiospermum</i> 9	x			
Caryophyllaceae 5, 7, 8, 9	x	x	x	x
<i>Cassipourea</i> 1	x			
<i>Catopsis</i> 1	x			
<i>Cavanillesia</i> 1	x			
<i>Cecropia</i> 3, 5, 6, 7, 8, 9, 10, 12	x	x	x	x
<i>Celtis</i> 2, 9, 10, 12	x		x	
<i>Cestrum</i> 6				x
Cheno-Am 1, 3, 8, 9, 10	x		x	x
<i>Cissus</i> 1	x			
<i>Clethra</i> 6				x
<i>Clusia</i> C.-type 7, 8		x		x
<i>Coccoloba</i> -type 1	x			
Combretaceae-Melastomataceae 3, 9	x			
<i>Combretum</i> 1	x			
Compositae 1, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12	x	x	x	x
<i>Compsonaura</i> 1	x			
<i>Conocarpus</i> 1	x			
<i>Copaifera</i> 1, 5	x		x	
<i>Cordia</i> 6, 9, <i>C. alliodora</i> 1	x			x
<i>Coriaria</i> 8				x
<i>Couroupita</i> 1	x			
<i>Croton</i> : Crotonoideae 1, 7, 8, 9	x	x		x
Cruciferae 7, 8		x		x
<i>Cupania</i> 1	x			
<i>Cuphea</i> 12			x	
<i>Curatella</i> 12			x	
<i>Daphnopsis</i> 6, 7		x		x
<i>Dialyanthera</i> 1	x			
<i>Didymopanax</i> 2, 7, 10, 12		x	x	
<i>Dodonaea</i> 6, 7, 8		x		x
<i>Dorstenia</i> 9	x			
<i>Drepanocarpus lunatus</i> -type 1	x			
<i>Drimys</i> 6, 7, 8, 9, 11	x	x		x
ERA 9, 10, 12	x		x	
Ericaceae 1, 4, 5, 6, 7, 8, 9, 11	x	x	x	x
<i>Erythrina</i> 1	x			
<i>Escallonia</i> 7		x		
<i>Eugenia</i> 9	x			

Appendix 2. Continued.				
Taxon	Lowland Central America	Upland Central America	Lowland South America	Upland South America
<i>Euphorbia</i> 8				x
<i>Ficus</i> 2, 9, 10, 12	x		x	
<i>Faramea</i> 1	x			
<i>Fuchsia</i> 7, 8		x		x
<i>Gaiadendron</i> 6, 7, 8		x		x
<i>Galium</i> 8				x
Gentianaceae 7		x		
<i>Geranium</i> 7, 8		x		x
cf. <i>Glycydendrum</i> 1	x			
<i>G. amazonicum</i> 1	x			
<i>Gomphrena</i> 9	x			
<i>Guazuma</i> 9	x			
<i>Gunnera</i> 7		x		
<i>Gryanthera darienensis</i> -type 1	x			
<i>Hedyosmum</i> 1, 3, 4, 5, 6, 7, 8, 9, 12	x	x	x	x
<i>Heliocarpus</i> 6, 7, 8		x		x
<i>Hesperomeles</i> 6, 7		x		x
<i>Hibiscus</i> 9	x			
<i>Hieronyma</i> 1, 6, 7, 8, 10	x	x	x	x
<i>Hippocratea volubilis</i> 1	x			
<i>Humiria</i> 5			x	
<i>Hura</i> 3, 5	x		x	
<i>Hydrangea</i> 1	x			
<i>Hydrocotyle</i> 8				x
<i>Hydrophila</i> 9	x			
<i>Hypericum</i> 6, 7, 8		x		x
<i>Ilex</i> 1, 4, 5, 6, 7, 8, 9, 12	x	x	x	x
<i>Ipomoea</i> 1	x			
<i>Juglans</i> 6, 8, 9	x			x
<i>Jussiaea</i> 1	x			
<i>Justicia</i> 1	x			
Labiatae 8, 12			x	x
<i>Lafoensia</i> 1	x			
<i>Laguncularia</i> 9	x			
Lecythidaceae- <i>Eschweilera</i> 5			x	
Leguminosae 2, 4, 5, 8, 10			x	x
Caesalpinioideae 5			x	
Mimosoideae 1, 9, 10	x		x	
<i>Leucaena multicapitula</i> 1	x			
<i>Licania arborea</i> 1	x			
<i>Limnocharis</i> 3	x			
<i>Liquidambar</i> 9	x			
<i>Liriosma</i> 1	x			
Loranthaceae 7, 12		x	x	
<i>Luehea</i> 1, 9	x			
<i>Lysipomia</i> 7		x		
Lythraceae 8				x
<i>Mabea</i> 1	x			
<i>Machaerium-Dalbergia</i> 5			x	
<i>Malouetia</i> 1	x			
Malpighiaceae 1, 8, 9, 10, 12	x		x	x

Appendix 2. Continued.

Taxon	Lowland Central America	Upland Central America	Lowland South America	Upland South America
Malvaceae 1, 8, 9	x			x
<i>Manihot</i> 1	x			
<i>Maripa</i> 1	x			
Melastomataceae-Combretaceae 1, 2, 4, 5, 6, 7, 8, 10	x	x	x	x
Meliaceae-Sapotaceae 1, 3, 5, 9, 12	x		x	
<i>Mendoncia</i> 1	x			
Menispermaceae 1	x			
<i>Merremia</i> 1	x			
<i>Miconia</i> 6, 8, 12			x	x
<i>Montia</i> 7		x		
Moraceae, Urticaceae, Urticales 1, 2, 3, 4, 5, 6, 7, 8, 9, 10	x	x	x	x
<i>Mortoniiodendron</i> 9	x			
<i>Mucuna</i> 1	x			
<i>Mollugo</i> 1	x			
<i>Myrica</i> 1, 3, 5, 6, 7, 8	x	x	x	x
<i>Myriophyllum</i> 8				x
<i>Myrrhiodendron-Niphogenton</i> 7		x		
Myrtaceae 1, 3, 4, 5, 6, 7, 12	x	x	x	x
<i>Ochroma</i> 1	x			
<i>Oreopanax</i> 7		x		
<i>Oryctanthus</i> 1	x			
<i>Ouratea O. guatemalensis</i> 1, 12	x		x	
Onagraceae 9	x			
<i>Pachira</i> 1	x			
<i>Pacouria</i> 1	x			
<i>Paullinia</i> 1	x			
<i>Panopsis</i> 8				x
<i>Pelliceria</i> 9	x			
<i>Phyllanthus</i> 1	x			
<i>Pilea P. trema</i> 2, 5, 6, 8			x	x
<i>Piper</i> 9, 10	x		x	
Piperaceae 1, 2, 4, 5, 7	x	x	x	
<i>Plantago</i> 7, 8, 9	x	x		x
Polygalaceae 1, 6, 8, 12	x		x	x
<i>Polygonum</i> 1, 7, 8, 9	x	x		x
<i>Polylepis-Acaena</i> 6, 8				x
Pontederiaceae 1	x			
Portulacaceae 1, 8	x			x
Proteaceae 4, 5, 6			x	x
<i>Pseudobombax</i> 1	x			
<i>Psidium</i> 9	x			
<i>Pterocarpus</i> -type 1	x			
<i>Puya</i> 7		x		
<i>Quararibea</i> 1	x			
<i>Quassia</i> 1	x			
<i>Quercus</i> 3, 5, 6, 7, 8, 9, 11	x	x	x	x
<i>Randia</i> 1	x			
Ranunculaceae 7, 8, 12		x	x	x
<i>Rapanea</i> R.-type 5, 6, 7, 8, 9	x	x	x	x
<i>Rauwolfia</i> 1	x			
<i>Relbunium</i> 8				x
<i>Rhizophora</i> 1, 9	x			

Appendix 2. Continued.				
Taxon	Lowland Central America	Upland Central America	Lowland South America	Upland South America
Rosaceae 9, 10	x		x	
Rubiaceae 1, 7, 12	x	x	x	
<i>Rumex costaricensis</i> 7		x		
<i>Salix</i> -S.-type 7, 9	x	x		
<i>Sapium</i> 1, 2, 7, 8, 12	x	x	x	x
S.-type 1, 9	x			
Sapotaceae 5			x	
Scrophulariaceae 8				x
<i>Sechium edule</i> -type 1	x			
Solanaceae 7, 8, 10, 12		x	x	x
<i>Spondias</i> -type 9	x			
<i>Styloceras</i> 6, 8				x
<i>Swartzia panamensis</i> -type 1	x			
<i>Symphonia</i> 1, 4, 5, 9, 12	x		x	
<i>Symplocos</i> Symplocaceae 1, 5, 6, 8	x		x	x
<i>Tabernaemontana</i> 1	x			
<i>Tetracera</i> 1	x			
<i>Thalictrum</i> T.-type 8, 9	x			x
Tiliaceae 4, 5			x	
<i>Tournefortia</i> 9	x			
<i>Trema</i> 2, 5, 9, 10	x		x	
<i>Trichanthera</i> 1	x			
<i>Tristicha</i> 1	x			
<i>Ulmus</i> 7, 9	x	x		
Umbelliferae 9, 10, 11	x	x	x	
<i>Utricularia</i> 1	x			
<i>Valeriana</i> 7		x		
<i>Vallea</i> 6				x
<i>Viburnum</i> 6, 7, 8		x	x	x
<i>Virola</i> 1, 9	x			
<i>Vochysia</i> 1	x			
<i>Weinmannia</i> W.-type 4, 5, 6, 7, 8, 9, 10, 12	x	x	x	x
<i>Zanthoxylum</i> 1, 9	x			
<i>Zea</i> 1, 2, 10	x		x	